Invasion hotspots and ecological saturation of streams across the Hawaiian archipelago

by

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Abstract. – Species introductions are a widely recognized threat to global freshwater biodiversity. The proliferation of non-native species can result in the loss of native species through direct and indirect interactions with predators, competitors, pathogens and parasites. Thus identifying invasion hotspots and understanding the capacity of vulnerable ecosystems to absorb new invasions is fundamental to conserving native biodiversity and preventing further introductions. Here, we assess whether endemic biodiversity, land-use and human population density predict the location of invasion hotspots and ecological saturation in streams across the Hawaiian archipelago. We found that non-native fishes, mollusks, crustaceans, and insects are prevalent in Hawaiian streams across the archipelago, whereas the distributions of native species appear to be constrained by urbanization and habitat alteration. We detected a strong link between invasion hotspots and human population densities, and we found a positive relationship between the number of non-native species and native species present in watersheds, suggesting that Hawaiian streams are not ecologically saturated. Though native species richness explained more than half of the variance in non-native mollusks and crustaceans, it explained a low proportion of the variance in non-native fish and insect richness, indicating that a compilation of factors influence total non-native species richness in Hawaiian streams. Our findings reveal that Hawaiian streams remain vulnerable to further species introductions, and that conservation of endemic Hawaiian stream fauna can be improved by addressing interactions between introductions and degradation that can arise from human habitation.

Résumé. – Les points chauds d'invasion et la saturation écologique de ruisseaux dans l'archipel hawaiien.

L'introduction d'espèces est une menace reconnue pour la biodiversité des eaux douces globales. La prolifération d'espèces allogènes peut conduire à la perte d'espèces indigènes en rapport avec les nouvelles interactions, directes et indirectes, avec les prédateurs, les compétiteurs, les pathogènes, et les parasites. Ainsi, l'identification de points chauds d'invasion et la compréhension de la capacité d'écosystèmes vulnérables à absorber l'invasion sont fondamentales pour la conservation de la biodiversité native et la prévention d'introductions dans le futur. Nous étudions si la biodiversité indigène, l'utilisation du terrain et la densité de la population humaine permettent de prédire la localisation de points chauds d'invasion et la saturation écologique dans les ruisseaux à travers l'archipel hawaiien. Nous avons trouvé que les poissons, mollusques, crustacés, et insectes allogènes sont prévalents dans les ruisseaux hawaiiens à travers l'archipel, alors que la distribution d'espèces indigènes semble être limitée par l'urbanisation et l'altération des habitats. Nous avons détecté un lien fort entre les points chauds d'invasion et la densité de la population humaine. De plus, nous avons trouvé une relation positive entre le nombre d'espèces allogènes et le nombre d'espèces indigènes présentes dans les lignes de partage des eaux, ce qui indique que les ruisseaux hawaiiens ne sont pas saturés écologiquement. Même si la richesse d'espèces indigènes explique plus de la moitié de la variance chez les mollusques et crustacés allogènes, elle explique une faible proportion de la variance pour les poissons allogènes et la richesse en insectes, ce qui suggère que plusieurs facteurs influencent la richesse totale d'espèces allogènes dans les ruisseaux hawaiiens. Nos découvertes révèlent que les ruisseaux hawaiiens restent vulnérables aux futures introductions d'espèces et que la conservation de la faune endémique des ruisseaux hawaiiens peut être améliorée par le traitement des interactions entre les introductions et la dégradation produite par l'habitat humain.

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Human-mediated species introductions are considered a major driver of global biodiversity loss (Vitousek *et al.*, 1997; Sala *et al.*, 2000; Butchart *et al.*, 2010). Native species can be lost as a consequence of direct (*e.g.* predation, competition) and indirect (*e.g.* habitat modification, transmission of novel pathogens) outcomes of species introductions (Mooney and Cleland, 2001; O'Dowd *et al.*, 2003; Prenter *et al.*, 2004; Charles and Dukes, 2008; Holitzki *et al.*, 2013; Gagne *et al.*, 2015, 2016). Imperilment depends, however, on factors that govern establishment and spread of non-native species, including community diversity. More diverse communities are expected to be more resistant to invasion (Elton, 1958) because competition for resources can increase with rising species diversity, *i.e.* ecological saturation (Tilman, 1997; Stachowicz and Tilman, 2005). Both fossil record and experiments provide evidence that greater diversity can impede invasion (reviewed in Stachowicz and Tilman, 2005). Spatial limitation in species rich communities, for instance, reduces invasion success and survival (Stachowicz *et al.*, 1999; Kennedy *et al.*, 2002; Mitchell and Knouft, 2009.) By extension, communities that are naturally depauperate may be especially susceptible to invasion due to greater resource availability for introduced species (Wilson, 1961; Sax and Brown, 2000; Sax *et al.*, 2002). Naturally depauperate communities also tend to harbour disproportionate numbers of endemic, rare, and at-risk species, which can elevate vulnerabilities to non-native species and increase the importance of conservation management (Levin *et al.*, 1996; Lyons and Schwartz, 2001).

Oceanic islands, which characteristically harbour low levels of native species richness and high levels of endemism, have proven to be exceptionally vulnerable to biological invasions (Myers *et al.*, 2000; O'Dowd *et al.*, 2003; Kier *et al.*, 2009). Some of the conditions that have given rise to endemic biodiversity on oceanic islands also increase the likelihood of invasion (MacArthur and Wilson, 1967; Simberloff and Wilson, 1969; Ziegler, 2002). Physical isolation, for example, promotes endemism but may constrain species richness. Physical isolation also can limit the exposure of endemic species to predators and diseases (Blackburn *et al.*, 2004; Whittaker and Fernández-Palacios, 2007); endemic species are thus oftentimes at a disadvantage when interacting with non-native species due to absent or limited defences (Sax *et al.*, 2002; Cambray, 2003; O'Dowd *et al.*, 2003; Charles and Dukes, 2008). Species losses from novel interactions are well documented (*e.g.* brown tree snake predation of avifauna on Guam, Savidge, 1987; the extinction of the Christmas Island rat from an introduced pathogen, Wyatt *et al.*, 2008). Accordingly, factors that elevate vulnerability, like so-called 'invasion meltdowns' (*i.e.* where past invasions enhance susceptibility to future invasions) are becoming ever more pressing concerns with the rising pace of species introductions (Simberloff and Von Holle, 1999; Gaston *et al.*, 2003; Simberloff, 2006; Charles and Dukes, 2008; Gillespie *et al.*, 2008; Ware *et al.*, 2014).

Terrestrial ecosystems across the Hawaiian archipelago illustrate the vulnerability of oceanic islands to biological invasions (Eldredge and Miller, 1995; Cincotta *et al.*, 2000). Terrestrial communities in Hawai'i historically exhibited ≥ 90% endemism (Zimmerman, 1948; Amadon, 1950; Carson and Kanehsiro, 1976; Carr and Kyhos, 1981; Myers, 1988; Paulay and Meyer, 2002), but proliferation of non-native species has driven both native terrestrial flora and fauna to extinction (Vitousek, 1988; D'Antonio and Dudley, 1995; Sax *et al.*, 2002; Asner *et al.*, 2008). For instance, the introduced carnivorous snail, *Euglandina rosea*, resulted in the extinction of the Hawaiian endemic land snail, *Achatinella mustelina* (Hadfield *et al.*, 1993). Species invasions also have contributed to habitat and geographical range contraction of native species. For example, the disappearance of native lowland forest on O'ahu has been attributed to the introduction of *Rattus exulans* (Athens, 2009). Novel competition and disease coupled with habitat conversion also now limit extant Hawaiian honeycreepers to high elevation habitat (Warner, 1968; Van Ripper *et al.*, 1986; Benning *et al.*, 2002).

Freshwater ecosystems in the Hawaiian archipelago also appear to be highly susceptible to invasion (Brasher *et al.*, 2006; Gagne *et al.*, 2015). Like terrestrial ecosystems, oceanic island freshwater ecosystems are characterized by low species richness and high endemicity (McDowall, 2003, 2004; Abell *et al.*, 2008; Alda *et al.*, 2016). The native aquatic macrofauna of Hawaiian streams, for example, consists of only five endemic fishes, four endemic gastropods, two endemic crustaceans and two native crustaceans (McDowall, 2010; Lindstrom *et al.*, 2012; Alda *et al.*, 2016). The geographic isolation of the Hawaiian archipelago has largely limited natural colonization of stream ecosystems to species capable of oceanic dispersal (McDowall, 2010; Alda *et al.*, 2016). Nearly all of the Hawaiian stream species exhibit an amphidromous life history; obligate amphidromous species mature and spawn in freshwater streams, but disperse through the ocean as larvae for up to six months. Facultative amphidromous species may forego marine dispersal in favour of remaining in freshwater (Hogan *et al.*, 2014). In contrast, intentional introductions for pest control and sport fishing as well as aquaria releases over the past 100+ years (Bryan, 1915; Yamamoto and Tagawa, 2000), have resulted in the establishment and spread of a diverse range of non-native species (Nico and Walsh, 2011). In streams on some islands, like O'ahu, the number of non-native aquatic species can be an order of magnitude higher than that of native aquatic species (Eldredge, 2000; Yamamoto and Tagawa, 2000).

There is mounting evidence that non-native species are contributing to the decline of native species in oceanic island

streams by altering and degrading habitat, preying upon vulnerable early life-stages, and transmitting novel pathogens (Brasher, 2003; Font, 2003; Walter *et al.*, 2012; Holitzki *et al.*, 2013; Gagne *et al.*, 2015; El-Sabaawi *et al.*, 2016). For example, extirpations of native *Megalagrion* damselflies on O'ahu – several of which are (or may soon come) under the protection of the U.S. Endangered Species Act – have been attributed to predation by introduced guppies and other poeciliids (Polhemus, 1993; Polhemus and Asquith, 1996; Englund, 1999; Yamamoto and Tagawa, 2000). Nonetheless, many native species exhibit adaptive traits, like waterfall climbing (Blob *et al.*, 2008, 2010; Maie *et al.*, 2012; Moody *et al.*, 2017), that can limit interactions with non-native species. By barring upstream movement of nearly all non-native species, features like shear waterfalls can create refugia for adults of some native amphidromous species (Blob *et al.*, 2010; Walter *et al.*, 2012). Refugia may not be sufficient protection, however, because early life stages (*i.e.* larvae drifting downstream and post-larvae recruiting upstream) must still traverse a gauntlet of predatory non-native fishes in lower stream reaches (Brasher, 2003; Walter *et al.*, 2012).

Increasing human habitation (*i.e.* population growth) and associated land-use intensification may be exacerbating the decline of native species in Hawaiian streams by creating conditions that favour non-native species (Schlosser, 1991; Wang *et al.*, 1997; McKinney, 2002; Marchetti *et al.*, 2004; Brasher, 2003, Walter *et al.*, 2012). Conditions on the island of O'ahu illustrate how population growth, urbanization, and non-native species can collectively imperil the endemic biota of oceanic island streams. O'ahu, which is home to 80% of the population of Hawai'i, has undergone extensive urbanization over the past century (Klasner and Mikami, 2003; Oki and Brasher, 2003), with Honolulu and outlying areas emerging as one of the most densely populated cities in the United States (Fulton *et al.*, 2001). Associated stream alterations (Brasher, 2003; Brasher *et al.*, 2004), such as channelization and water diversions, favour non-native species by reducing habitat heterogeneity and elevating water temperature (Schlosser, 1991; Moyle and Light, 1996; Scott and Helfman, 2001; Meador *et al.*, 2003). As is typical on tropical islands, stream modifications also are concentrated in urban areas at lower elevations (Resh *et al.*, 1992; Pringle and Ramirez, 1998; Brasher *et al.*, 2004), which can intensify the gauntlet that native diadromous species must navigate to complete their life cycle.

Identifying invasion hotspots (*i.e.* locations where conditions favour accumulative establishment of non-native species) and understanding whether at-risk ecosystems remain vulnerable to invasion can support conservation management and help prevent further introductions (Chapin *et al.*, 2000; Leprieur *et al.*, 2008). Here we examine the distribution of non-native and native species in streams across the Hawaiian archipelago to assess whether endemic biodiversity, land-use and human population density predict the location of invasion hotspots and ecological saturation. Leveraging archival data on stream biodiversity, land-use, and human population density across the Hawaiian archipelago, we first identified the number and location of invasion hotspots and then tested the hypotheses that non-native species richness corresponds to (1) human population densities, which serves as a proxy for anthropogenic pathways of introduction; (2) urbanization, which serves as a proxy for anthropogenic habitat disturbance; or (3) a combination of both human population and land-use. We also tested the hypotheses that invasion hotspots correspond to native diversity hotspots, and that streams with elevated total species richness (*i.e.* due to species invasions) have achieved ecological saturation (*i.e.* a plateau in species richness).

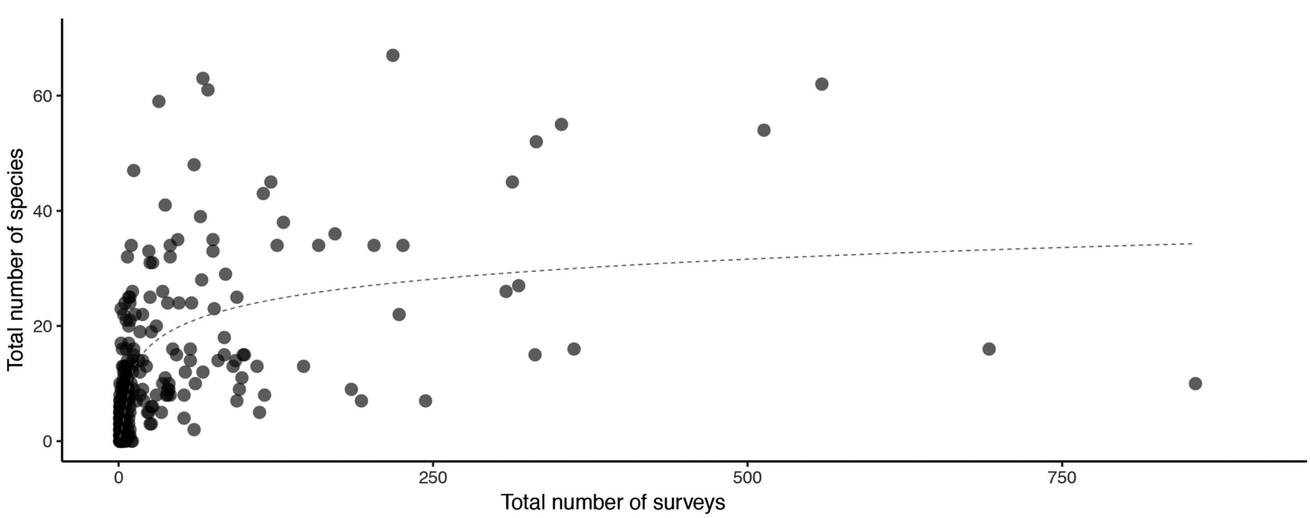

Figure 1. – Generalized linear model of sampling effort on species presence across all Hawaiian watersheds.

MATERIALS AND METHODS

Data compilation

We reconstructed archipelago-wide species distributions from online summaries presented by the Hawai'i Division of Aquatic Resources (DAR) in the Atlas of Hawaiian Watersheds and their Aquatic Resources (www.hawaiiwatershedatlas.com). The "DAR Atlas" is a compilation of species occurrence data from 12,040 in-stream surveys (mostly snorkel surveys, but also trapping surveys, impoundment surveys, rapid assessments, line transects, and general surveys) conducted from 1893 to 2008. The DAR Atlas includes both species presence/absence and abundance data. Since abundance data are not available for all species or watersheds, we restricted our analyses to presence/absence data from 331 watersheds. The availability of data for these watersheds varied according to the number of surveys completed between 1893 and 2008. Accordingly, we accounted for differences in sampling effort ($t_{1,330} = 9.79$; $P < 0.001$; Fig. 1) by including the number of surveys as a covariate in all analyses of species presence/absence data (Gotelli and Colwell, 2001).

Land-cover statistics were summarized from the DAR Atlas to evaluate the influence of land-use on the composition of stream communities across the archipelago. The DAR Atlas includes 30 m^2 resolution land-cover metrics for all watersheds based on remote sensing analyses conducted

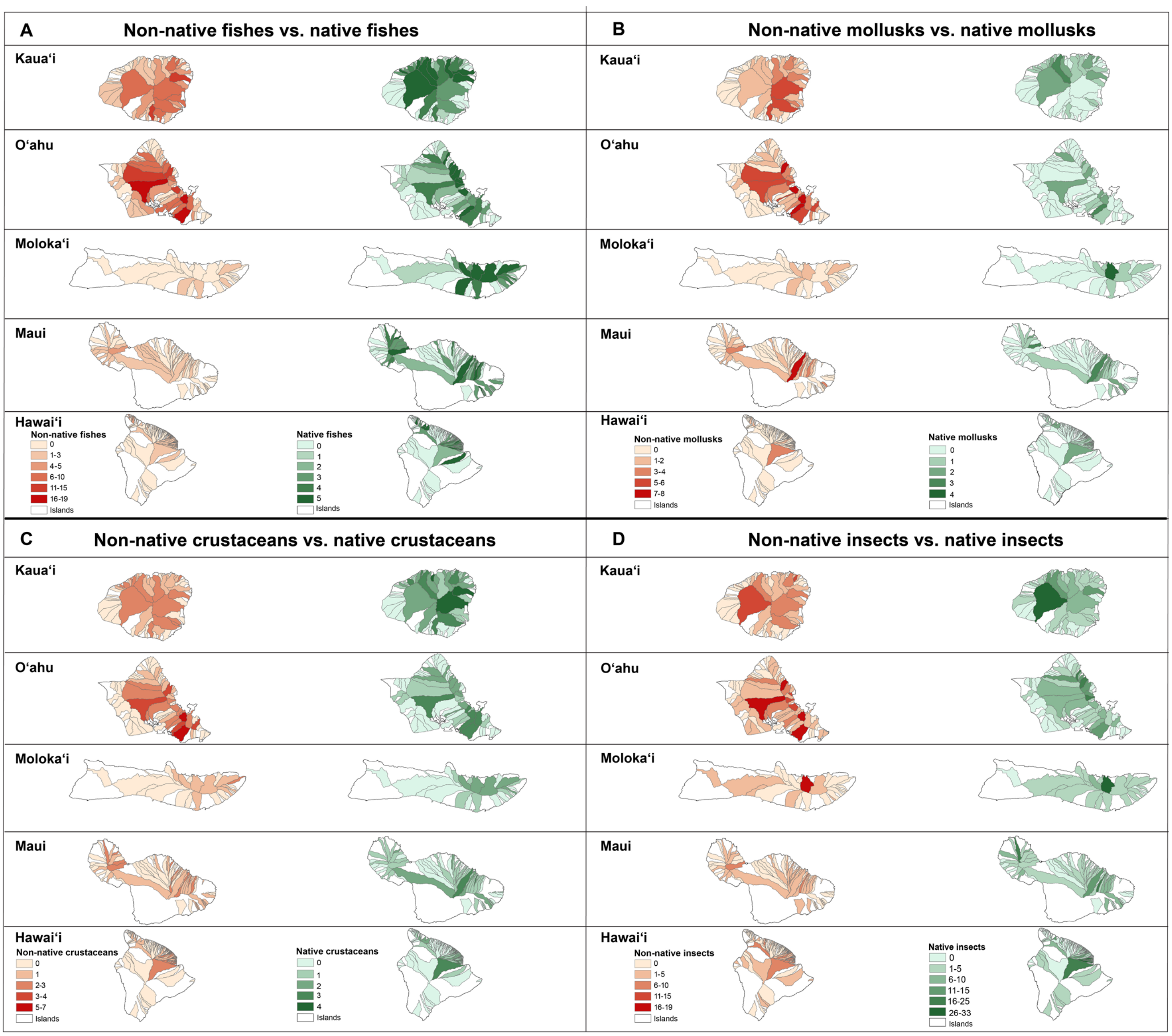

Figure 2. – Spatial distributions of non-native species (red) and native species (green) across all Hawaiian watesheds for each taxonomic group comparison. **A**: Non-native fishes vs. native fishes; **B**: Non-native mollusks vs. native mollusks; **C**: Non-native crustaceans vs. native crustaceans; **D**: Non-native insects vs. native insects. Islands are not to scale.

by the NOAA Coastal Change Analysis Program (https://coast.noaa.gov) and the Hawai'i Gap Analysis Program. For each of our 331 study watersheds, we examined land-cover percentages of high-density development (> 75% impervious surface in urban land-cover), low-density development (25-75% impervious surface in urban land-cover), cultivated land, grassland, scrub/shrub, evergreen forest, palustrine forest, palustrine scrub, palustrine emergent, estuarine forest, and bare land. We also examined watershed area and maximum elevation. Because we found evidence of collinearity and significant covariance between 34 pairs of variables (Annexe 1), we conducted a Principal Components Analysis (PCA) to identify dominant gradients of variation in watershed attributes across the archipelago (Pearson, 1901) in R 3.3.1 (R Core Team, 2014).

Human population attributes were assessed according to the 2010 census of Hawai'i (http://census.hawaii.gov/census_2010). Weighted population densities (persons/km^2) were calculated for each watershed from census blocks clipped to watershed boundaries. Unless otherwise noted, we used ArcGIS 10.3 (ESRI, 2016) to compile and examine all geographic information, including mapping species distributions based on presence/absence records (Fig. 2).

Influence of sampling effort, land-use and human demography on species richness

We relied on Redundancy Analysis (RDA) – a multiple linear regression ordination method (Rao, 1964) – to determine the relative influence of sampling effort, island, land-cover principal component 1 (PC1), land-cover principal component 2 (PC2), and human population density on faunal richness. We first divided non-native and native species into the following categories: fishes, mollusks, crustaceans, and insects (Annexe 2). Using the vegan package for R (Oksanen *et al.*, 2016), RDAs were then performed separately for each taxonomic group. We estimated the adjusted coefficient of determination (R^2_{adj}) for each explanatory variable. We used forward stepwise model selection with AIC to improve the fit of each model, and to reduce the likelihood of type I errors. Statistical significance of each predictor was determined using permutation tests to compare observed and randomized model R^2_{adj}. Since land-cover PC1 and weighted population densities were moderately correlated (Pearson's correlation: –0.56, $P < 0.001$), we conducted variance partitioning with partial RDAs to estimate the variance in species richness that is independently explained by each variable in the best-fit RDA model (Legendre, 2008; Peres-Neto and Legendre, 2010).

Hotspots and ecological saturation

Pooling species of all taxa, we conducted separate RDAs for non-native and native species to determine the best model structure for explaining species richness based on sampling effort, island, land-cover PC1, land-cover PC2, and human population density. Using the best-fit RDA models for non-native and native species, we identified invasion and native hotspots as watersheds in which the residual was at least two standard deviations above the mean. Similarly, we used

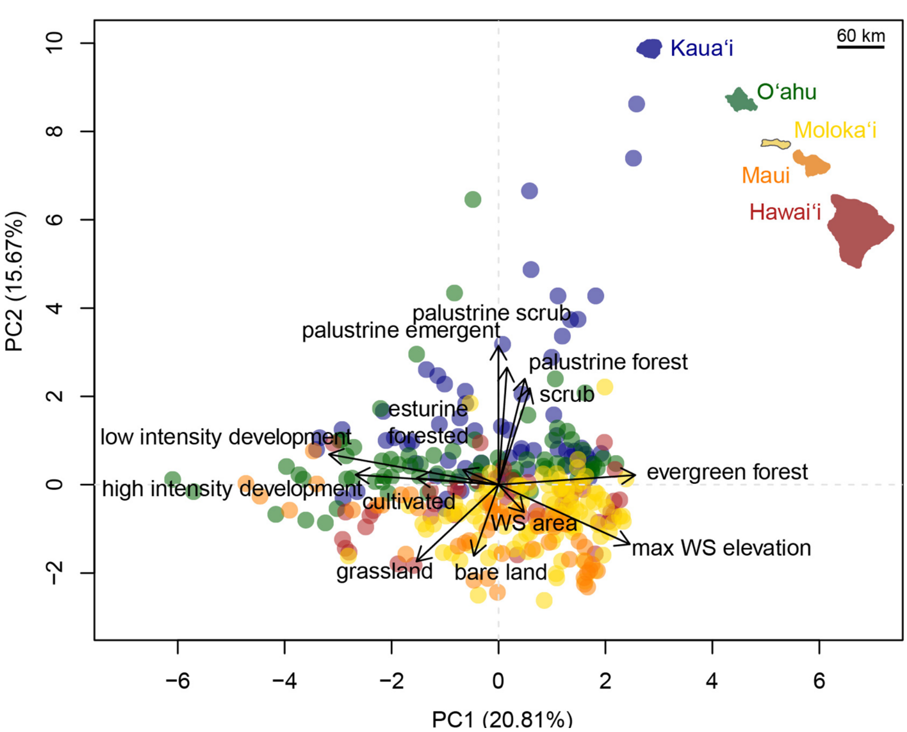

Figure 3. – Principal component analysis of land-cover and watershed variables across all Hawaiian watersheds.

Table I. – Principle component loadings of land-cover and watershed variables across all Hawaiian watersheds.

Land-cover categories	Loadings	
	PC1	PC2
Watershed area	0.080	–0.104
Maximum elevation	0.410	–0.225
High intensity development	–0.446	0.038
Low intensity development	–0.529	0.115
Cultivated	–0.256	0.025
Grassland	–0.256	–0.290
Scrub	0.098	0.365
Evergreen forest	0.426	0.036
Palustrine forest	0.082	0.400
Palustrine scrub	0.000	0.524
Palustrine emergent	0.026	0.442
Estuarine forest	–0.111	0.056
Bare land	–0.077	–0.269

the best-fit RDA model structure from each non-native and native taxon group to determine taxon-specific hotspots according to the same criteria.

Ecological saturation (*i.e.* the saturation point, or plateau, that bounds the upper limit of species diversity) can be inferred by comparing the number of non-native species against the number of native species in a given location (MacArthur and Wilson, 1963, 1967; Cornell and Lawton, 1992; Hubbell, 2001). We determined whether Hawaiian watersheds exhibit a plateau in species richness by determining the relationship between the number of non-native and native species using Generalized Linear Model Poisson regressions with a log link function in R. Hierarchical models to explain non-native species richness of each taxonomic group included the following predictors: native species richness, sampling effort, island, percentage of high elevation reach type, and number of streams in the watershed, which is a proxy measure of habitat heterogeneity and availability (Fausch *et al*., 2002; Torgersen *et al.,* 2008). We analyzed 322 watersheds in total; nine watersheds from the original 331 were dropped due to lack of data on stream reach elevation. Models were corrected for over-dispersion using the R package dispmod (Scrucca, 2012), and the best model was chosen based on AIC scores. We relied on measures of residual deviance to perform goodness-of-fit tests. The residual deviance is the difference between the deviance of the current model and the maximum deviance of the ideal model where the predicted values are identical to the observed values. Thus, if the residual difference is sufficiently small, the goodness-of-fit chi-squared test will not be significant, indicating that the model fits the data. Because the effect of island was always significant, we also conducted separate tests for each island.

RESULTS

The influence of sampling effort, land-use and human demography on species richness

The first PC factor recovered in the PCA of land-cover and watershed variables corresponded to a strong urban-to-forest land use and elevational gradient (Fig. 3; Tab. I). Notable loadings included high and low intensity urban development (–0.45 and –0.53, respectively), cultivated and grassland area (both –0.26), and evergreen forest and maximum elevation (0.43 and –0.41, respectively). Conditions on each island spanned PC1, though sites on O'ahu were skewed toward greater high-intensity urban land cover while Moloka'i, Maui, and Hawai'i were more forested. PC2 (Fig. 3; Tab. I) corresponded to grassland (–0.29) loading opposite to palustrine scrub, emergent and forest (0.53, 0.44 and 0.4, respectively). Palustrine scrub/emergent/forest cover and non-tidal, saline wetlands largely occur on wide valley floors, which are more characteristic of older islands (*i.e.* O'ahu and Kaua'i) than younger islands (*i.e.* Moloka'i, Maui, and Hawai'i).

The full RDA and the reduced RDA (rRDA) models explained 35-58% of the variance of species richness for all non-native taxonomic groups (Tab. II). All of the non-native rRDA models included human population density. However, human population density only explained a large proportion of the variance for non-native fish richness (Fig. 4; Tab. II). Variance partitioning indicated that non-native mollusk and insect richness reflected sampling effort, explaining 4.0% and 8.7%, respectively, as did the interaction of survey number with human population density (3.7% and 7.4%, respectively). Non-native mollusks were the only group for which the best-fit rRDA model excluded land-cover PC2; the rRDA instead included differences among islands (Fig. 4).

For each taxonomic group of native species, the full RDA and the best-fit rRDA models explained 32-48% of the variance of species richness (Tab. II). With the exception of native crustacea, sampling effort explained the largest proportion of the variance (15.5-16.7%) in all of the best-fit rRDAs. Land-cover PC2 explained the largest proportion of variance in the best-fit rDNA for native crustacea (8.0%). Land-cover PC1 or PC2 were the second largest contributors to the best-fit rRDA for fishes, mollusks, and insects (1.5-6.1%). Land-cover PC2 was an explanatory factor in the best-fit rRDA models for all native taxa except insects; the rRDA for insects included land-cover PC1 instead of PC2. Human population density only contributed to the native fish and insect rRDAs (2.1% and 1.7%, respectively; Fig. 4).

Hotspots and ecological saturation

We identified 37 invasion hotspots across the Hawaiian archipelago (Annexe 3). Half of the invasion hotspots are on O'ahu (19 of 37), with 11 located on the windward side of

Table II. – Redundancy analysis (RDA) for each taxonomic group. Results of the full model RDAs and the RDAs with forward selection for best-fit model determination. Bold indicates the best-fit model for each taxonomic group.

Taxonomic group	Global RDA (Number of surveys * Island * Land-cover PC1 * Land-cover PC2 * Human population density)			Forward selection	AIC	R^2_{adj}	F	*P*
	R^2_{adj}	F	*P*					
Non-native fishes	0.351	11.38	< 0.001	Human population density	637	0.176	71.58	0.002
				Human population density + Island	610	0.243	30.09	0.002
				Human population density + Island + Land-cover PC2	**607**	**0.253**	**5.61**	**0.016**
Non-native mollusks	0.561	12.31	< 0.001	Human population density	209	0.114	43.38	0.002
				Human population density + Number of surveys	184	0.181	28.05	0.002
				Human population density + Number of surveys + Island	165	0.229	21.43	0.002
				Human population density + Number of surveys + Island + Human population density * Number of surveys	150	0.267	17.45	0.004
				Human population density + Number of surveys + Island + Human population density * Number of surveys + Number of surveys * Island	**139**	**0.292**	**13.12**	**0.002**
Non-native crustaceans	0.412	6.75	< 0.001	Human population density	–15	0.069	25.74	0.002
				Human population density + Land-cover PC2	–18	0.080	4.681	0.032
				Human population density + Land-cover PC2 + Human population density*Land-cover PC2	**–30**	**0.117**	**14.805**	**0.002**
Non-native insects	0.578	13.20	< 0.001	Number of surveys	712	0.142	55.72	0.002
				Number of surveys + Human population density	672	0.239	42.97	0.002
				Number of surveys + Human population density + Land-cover PC2	642	0.311	35.18	0.002
				Number of surveys + Human population density + Land-cover PC2 + Number of surveys * Human population density	627	0.343	16.81	0.002
				Number of surveys + Human population density + Land-cover PC2 + Number of surveys * Human population density + Number of surveys * Land-cover PC2	**619**	**0.361**	**10.13**	**0.016**
Native fishes	0.480	8.92	< 0.001	Number of surveys	299	0.265	120	0.002
				Number of surveys + Land-cover PC1	284	0.300	17.58	0.002
				Number of surveys + Land-cover PC1 + Land-cover PC2	270	0.331	16.14	0.002
				Number of surveys + Land-cover PC1 + Land-cover PC2 + Human population density	254	0.363	17.18	0.002
				Number of surveys + Land-cover PC1 + Land-cover PC2 + Human population density + Number of surveys * Land-cover PC1	**245**	**0.380**	**10.00**	**0.002**
Native mollusks	0.316	4.448	< 0.001	Number of surveys	-253	0.188	77.44	0.002
				Number of surveys + Land-cover PC2	**-258**	**0.203**	**7.33**	**0.008**
Native crustaceans	0.351	5.208	< 0.001	Land-cover PC2	-44	0.052	19.13	0.002
				Land-cover PC2 + Number of surveys	-46	0.060	3.85	0.046
				Land-cover PC2 + Number of surveys + Land-cover PC2 * Number of surveys	**-58**	**0.097**	**14.25**	**0.002**
Native insects	0.386	6.06	< 0.001	Number of surveys	1039	0.212	89.9	0.002
				Number of surveys + Land-cover PC1	1030	0.233	9.77	0.006
				Number of surveys + Land-cover PC1 + Human population density	**1025**	**0.250**	**8.26**	**0.01**

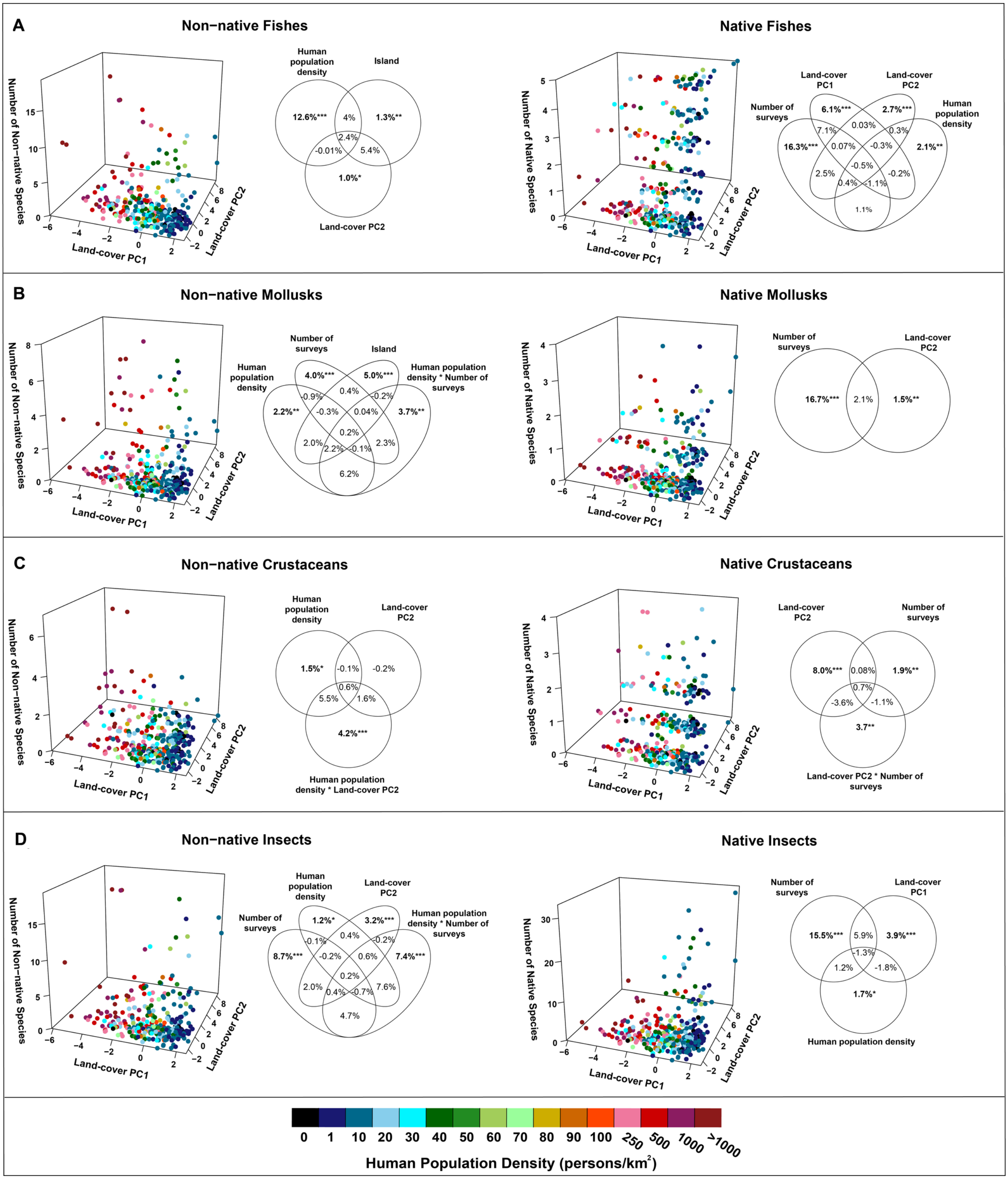

Figure 4. – Variance partitioning of explanatory variables from each best-fit redundancy analysis model of species richness for each taxonomic group. **A**: Non-native fishes vs. native fishes; **B**: Non-native mollusks vs. native mollusks; **C**: Non-native crustaceans vs. native crustaceans; **D**: Non-native insects vs. native insects. Coefficient significance is indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

the Ko'olau Range. We detected three hotspots in the northern Ko'olau Loa section of the mountain range, and eight in the southern Ko'olau Poko section of the mountain range. The remaining invasion hotspots on O'ahu are located in three North Shore watersheds (Ki'iki'i, Paukauila, and Anahulu), as well as the Waikele and Waiawa watersheds that drain portions of the leeward side of the Ko'olau Range and the windward side of the Waianae Range into Pearl Harbor, and the Makaha watershed in the Waianae Range. Eight invasion hotspots are located on the windward side of Kaua'i across the Hanalei, Līhu'e, and Koloa regions. Only one invasion hotspot was found on Maui, corresponding to the Wailau Iki West watershed on the windward side of the island. Nine invasion hotspots are located on Hawai'i, all within the Hilo region except for Waikola watershed in the Hamakua region and Waiulaula watershed in the Kohala region. Just under half (18 of 37) of the invasion hotspots are in watersheds with higher than average human population densities (50-1027 persons/km^2), including eleven on O'ahu.

We identified 37 native biodiversity hotspots across the archipelago (Annexe 3). The majority (25 of 37) of the hotspots are located on the islands of Maui and Hawai'i. On Maui, all nine hotspots are located on the windward side of the island: two are located within the West Maui Forest Reserve (Honokōhau and Makamakaole watersheds), and seven are located in protected lands on the eastern side of the island; three hotspots occur in the Ko'olau Forest Reserve, two occur in the Hanawai Nature Forest Reserve, and two occur in Haleakalā National Park. On Hawai'i, all 16 native biodiversity hotspots are on the Hamakau coast. Of the remaining 12 native hotspots, three are located in the windward Hanalei and Līhu'e regions of Kaua'i, and eight are on O'ahu, with the majority located on the windward side of the Ko'olau Range. One native biodiversity hotspot is located on Moloka'i. The majority (26 of 37) native biodiversity hotspots are located in forested watersheds. Only seven of 37 native hotspots are in watersheds with higher than average human population densities, including four on O'ahu.

We identified 15 watersheds that corresponded to invasion and native biodiversity hotspots, with most occurring on O'ahu and Hawai'i (six on each). Considering each taxonomic group separately, insects are the primary driver of congruency among invasion and native hotspots in watersheds on O'ahu and Hawai'i, though fishes are also responsi-

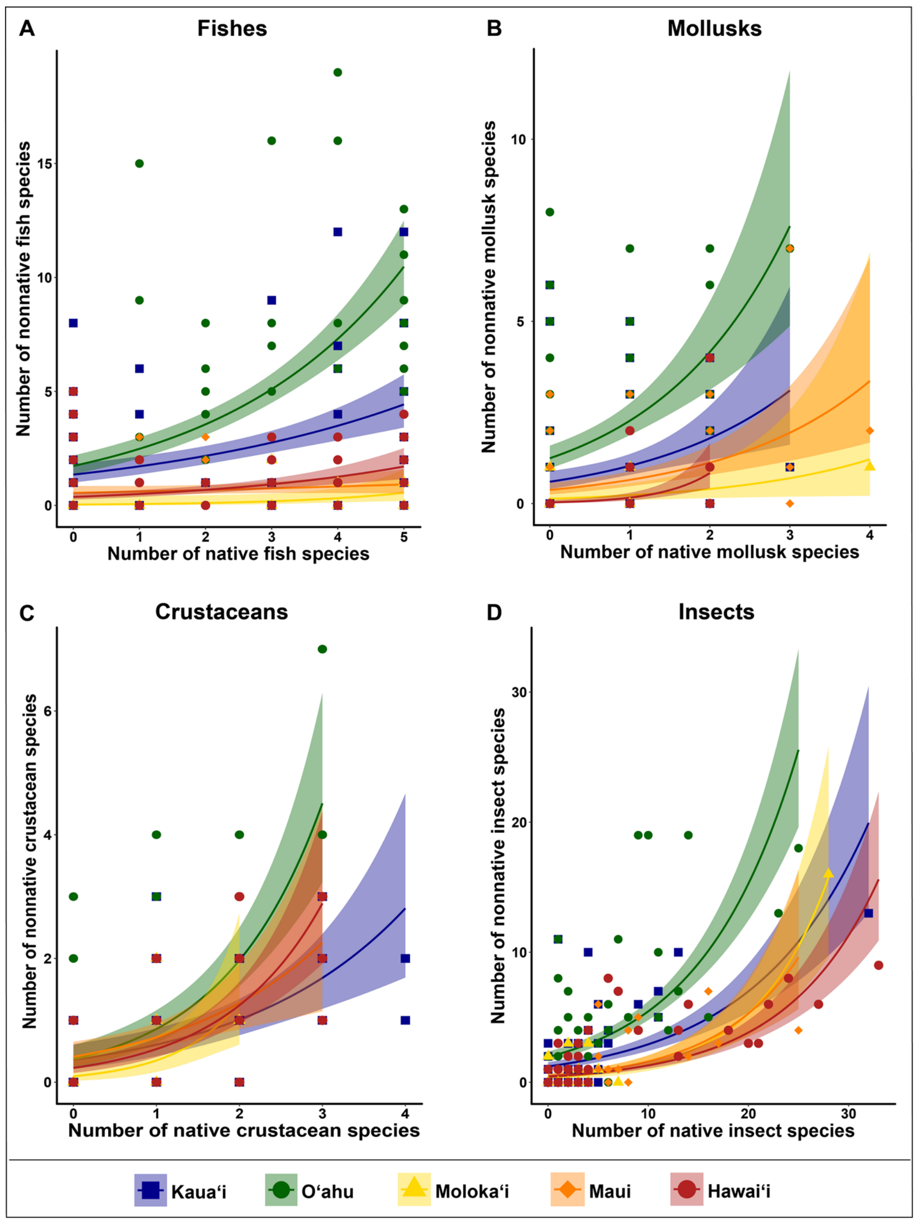

Figure 5. – Generalized linear models of non-native species richness vs. native species richness of each island for each taxonomic group. **A**: Non-native fishes vs. native fishes; **B**: Non-native mollusks vs. native mollusks; **C**: Non-native crustaceans vs. native crustaceans; **D**: Non-native insects vs. native insects.

Table III. – Generalized linear models with forward selection for best-fit model determination for each non-native to native taxonomic group comparison across all islands. Bold indicates the best-fit model for each taxonomic group. Coefficient significance is indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Taxonomic comparisons	Generalized linear models	df	AIC	X^2 *goodness of fit P*-values	Parameter	Coefficient
Non-native fishes vs. native fishes	Native species	320	1395			
	Native species + Island	319	1220			
	Native species + Island + Number of surveys	318	1222			
	Native species + Island + Number of surveys + Number of streams	317	1183			
	Native species + Island + Number of surveys + Number of streams + % of high elevation reaches	**316**	**1122**	**0.99**	Native species	0.273***
					Island	–0.254***
					Number of surveys	–0.001
					Number of streams	0.105***
					% of high elevation reaches	–0.013***
Non-native mollusks vs. native mollusks	Native species	320	821			
	Native species + Island	319	740			
	Native species + Island + Number of surveys	318	736			
	Native species + Island + Number of surveys + Number of streams	317	729			
	Native species + Island + Number of surveys + Number of streams + % of high elevation reaches	**316**	**717**	**0.99**	Native species	0.599***
					Island	–0.378***
					Number of surveys	0.003**
					Number of streams	0.122***
					% of high elevation reaches	–0.009*
Non-native crustaceans vs. native crustaceans	**Native species**	**320**	**622**	**0.99**	Native species	0.695***
	Native species + Island	319	624			
	Native species + Island + Number of surveys	318	624			
	Native species + Island + Number of surveys + Number of streams	317	626			
	Native species + Island + Number of surveys + Number of streams + % of high elevation reaches	316	623			
Non-native insects vs. native insects	Native species	320	1243			
	Native species + Island	319	1139			
	Native species + Island + Number of surveys	318	1131			
	Native species + Island + Number of surveys + Number of streams	317	1131			
	Native species + Island + Number of surveys + Number of streams + % of high elevation reaches	**316**	**1110**	**0.99**	Native species	0.170***
					Island	–0.218***
					Number of surveys	0.001
					Number of streams	0.043
					% of high elevation reaches	–0.010***

Table IV. – Best-fit generalized linear models with forward selection for each non-native to native taxonomic group comparison for each island. Coefficient significance is indicated by * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Comparison	Island	df	Model parameters	Coefficient
Non-native fishes vs. native fishes	Kaua'i	52	Native species	0.299*
			Number of Surveys	–0.003
			Number of streams	0.125*
			% of high elevation reaches	–0.017**
	O'ahu	56	Native species	0.399**
			Number of Surveys	–0.001
			Number of streams	0.081
			% of high elevation reaches	0.004
	Moloka'i	21	Native species	0.732
			Number of Surveys	–0.013
			Number of streams	0.098
			% of high elevation reaches	0.001
	Maui	65	Native species	–0.122
			Number of Surveys	0.010**
			Number of streams	–0.022
			% of high elevation reaches	–0.006
	Hawai'i	103	Native species	0.305**
			Number of Surveys	–0.001
			Number of streams	0.086
			% of high elevation reaches	–0.019**
Non-native mollusks vs. native mollusks	Kaua'i	52	Native species	0.791*
			Number of Surveys	–0.001*
			Number of streams	0.139
			% of high elevation reaches	–0.011
	O'ahu	56	Native species	0.577*
			Number of Surveys	–0.005*
			Number of streams	0.147*
			% of high elevation reaches	–0.012
	Moloka'i	21	Native species	0.589
			Number of Surveys	0.006
			Number of streams	0.206
			% of high elevation reaches	0.059
	Maui	65	Native species	0.353*
			Number of Surveys	0.010
			Number of streams	0.041
			% of high elevation reaches	0.017
	Hawai'i	103	Native species	1.516***
			Number of Surveys	–0.003
			Number of streams	0.125*
			% of high elevation reaches	0.013
Non-native crustaceans vs. native crustaceans	Kaua'i	52	Native species	0.511***
	O'ahu	56	Native species	0.845***
	Moloka'i	21	Native species	1.297**
	Maui	65	Native species	0.567***
	Hawai'i	103	Native species	0.844**

ble for the congruency of particular hotspots (*i.e.* Kapa'a on Kaua'i and Kaluanui on O'ahu). Designation of Nanue watershed on Hawai'i as an invasion and native biodiversity hotspot reflects contributions of all four taxonomic groups. Only Waikele watershed on the leeward side of the Ko'olau Range on O'ahu is identified as a hotspot for all four taxonomic groups independently in both native and non-native species. Of the 15 congruent hotspots, four exhibit higher than average human population densities, including three on O'ahu (Kāne'ohe, Waikele, and Nu'uanu) and one on Kaua'i (Kapa'a). The majority (9 of 15) of the watersheds are forested; all others are urbanized (Annexe 3).

With the exception of crustacea, the best GLM for non-native species included all five predictor variables (Tab. III). The crustacean model was not improved by adding variables beyond the number of native species. In all cases, the chi-squared goodness of fit analyses was non-significant, indicating that the models fit the data reasonably well. In all comparisons, the number of non-native species was positively and significantly related to the number of native species (Tab. III). Non-native species counts were positively and significantly related to the number of streams within each watershed for fishes and mollusks. Non-native species counts were positively and significantly related to sampling effort for mollusks. The percentage of high elevation reaches (*i.e.* upstream reaches and headwaters) and island age (*i.e.* oldest to youngest) on the other hand, were significantly negatively related to non-native species richness for all taxonomic groups except crustacea.

The effect of each variable differed among islands (Fig. 5; Tab. IV). With the exception of fishes on Maui and Moloka'i and mollusks

Table IV. – Continued.

Comparison	Island	df	Model parameters	Coefficient
Non-native insects vs. native insects	Kaua'i	52	Native species	0.374***
			Number of Surveys	–0.004
			Number of streams	–0.018
			% of high elevation reaches	–0.026***
	O'ahu	56	Native species	0.170***
			Number of Surveys	–0.002
			Number of streams	0.061
			% of high elevation reaches	–0.015*
	Moloka'i	21	Native species	0.053**
			Number of Surveys	0.004
			Number of streams	0.241*
			% of high elevation reaches	–0.054**
	Maui	65	Native species	0.089***
			Number of Surveys	0.006*
			Number of streams	–0.026
			% of high elevation reaches	0.0434***
	Hawai'i	103	Native species	0.129***
			Number of Surveys	0.001
			Number of streams	0.041
			% of high elevation reaches	0.029*

on Moloka'i, the number of native species was a significant predictor of the number of non-native species on all islands. The percentage of high elevation reaches was associated with lower non-native fish richness on Kaua'i and Hawai'i, and lower non-native insect richness on Kaua'i, O'ahu, and Moloka'i, whereas it was associated with higher non-native insects on Maui and Hawai'i. The number of streams had a positive relationship with non-native fish richness on Kaua'i, non-native mollusks on O'ahu and Hawai'i, and non-native insects on Moloka'i. Sampling effort was positively associated with non-native fish and insect richness on Maui and negatively associated with non-native mollusk richness on Kaua'i and O'ahu.

DISCUSSION

Our results illustrate that non-native species are pervasive in Hawaiian streams, and that invasion hotspots are concentrated in highly populated urban areas on O'ahu. However, the longitudinal distribution of non-native species within rivers is limited by elevation and other physical characteristics of watersheds (Brasher *et al.*, 2006). The converse pattern was observed for native species; intensive land-use (*i.e.* urbanization and deforestation) rather than elevation appears to constrain distributions. Nonetheless, invasion hotspots and native biodiversity hotspots show broad concordance, which corresponded to a positive correlation between non-native and native species richness across the archipelago. This suggests that Hawaiian streams are not ecologically saturated, but instead remain vulnerable to further species introductions.

Like terrestrial invaders that often draw more scientific attention, aquatic invasive species are recognized as a principle threat to endemic biodiversity (Simberloff, 1995; Ricciardi and Macisaac, 2010), including the endemic stream fauna of the Hawaiian archipelago (Brasher, 2003). Our results demonstrate that non-native species are prevalent on all of the high islands with perennial streams (Fig. 2). Although we also found endemic species to be widely distributed, the occurrence records for amphidromous fishes and aquatic invertebrates may be misleading. Recent surveys (Blum *et al.*, 2014) indicate that widely-distributed amphidromous species often occur at low population densities in highly populated regions of the archipelago like O'ahu. The combination of variation in population carrying capacity among watersheds (and perhaps entire islands) and pelagic larval dispersal likely gives rise to source-sink dynamics that sustain at-risk populations (Brasher *et al.*, 2004; Blum *et al.*, 2014). Genetic and demographic evidence from archipelago-wide population surveys also suggests that source-sink networks either do not span multiple islands or that the influx of off-island immigrants exerts little influence on local demography (Blum *et al.*, 2014; Hogan *et al.*, 2014). Thus, local populations of endemic species may be more susceptible to extirpation as a result of species invasions than would appear from archival occurrence records like those used in this study, particularly in areas with concentrations of invasion hotspots like O'ahu.

We found that the distribution of non-native species is associated more closely with human demography than with land-use (Fig. 4; Tab. II). The majority of invasion hotspots corresponded to watersheds on O'ahu with high human population densities (> 100 person/km^2). This accords with other findings that invasions hotspots often result from cumulative introductions associated with anthropogenic transport pathways and hubs (*e.g.* Drake and Lodge, 2004; Lockwood *et al.*, 2005). As many of the introduced fishes and invertebrates are widely available in the aquarium hobby trade (*e.g.* mollies, guppies, catfish, cichlids), we suspect that aquarium releases govern propagule pressure of species introductions

in the Hawaiian archipelago, particularly on O'ahu, which harbours introduced species that are rarely observed on other islands. Accidental and intentional introductions undoubtedly also contribute to the propagule pressure of non-native species with utilitarian (*e.g.* pest control) and economic value (*e.g.* aquaculture, sport fishing). Intensive land-use was also associated with non-native species distributions, suggesting that changes in water quality, hydrology, and other associated in-stream modifications can facilitate the establishment and spread of non-native aquatic species (Brown, 2000; McKinney, 2002; Brasher *et al.*, 2006).

Our results affirm that the endemic biota of Hawaiian streams also face multiple interacting threats from human habitation and land-use intensification (Brasher, 2003; Naeem *et al.*, 2012; Walter *et al.*, 2012; Blum *et al.*, 2014). We found that native stream species richness is negatively related to population densities and urbanization, particularly at lower elevations (Fig. 4; Tab. II). These relationships likely reflect the prevalence of associated hydrological and geomorphological interventions – ranging from bed channelization to surface water diversions – intended to safeguard infrastructure and sustain land-use development. Consequences include the loss of riparian vegetation and surface erosion, which can inhibit algal growth and grazing by elevating turbidity (Kido, 1996). Stream alterations can be especially detrimental to endemic amphidromous species that migrate between freshwater and marine environments. For example, fish and invertebrate larvae drifting downstream can be entrained in diversions and ditches. Similarly, dry stream reaches resulting from surface water diversion can impede the movement of both drifting larvae and juveniles recruiting upstream. Restricted emigration and immigration can, in turn, reduce local abundance and increase the likelihood of extirpation (Brasher, 1996, 2003; Walter *et al.*, 2012; Blum *et al.*, 2014). Concomitant changes in physical (*e.g.* temperature) and chemical (*e.g.* dissolved oxygen, nutrient loading) characteristics also can increase exposure of early life stages to stressors as well as reduce the amount of suitable adult habitat. Outcomes of human habitation and land-use intensification are most evident on O'ahu, where several intolerant species (*e.g. Lentipes concolor* (Gill, 1860), *Neritina granosa* Sowerby, 1825, *Sicyopterus stimpsoni* (Gill, 1860)) have been nearly extirpated (Fitzsimons *et al.*, 1990; Higashi and Yamamoto, 1993; Blum *et al.*, 2014).

The striking correspondence between invasion hotspots and native biodiversity hotspots runs contrary to the expectation that ecological opportunities for invasion should be ubiquitous because of the paucity of native biodiversity in Hawaiian Island streams (Elton, 1958; Fox and Fox, 1986). The observed relationships between non-native and native species diversity suggest that, even in depauperate systems, invasions are more likely to proceed in watersheds with higher native species diversity. In all but two of the 'dual hotspot' watersheds, at least three species of endemic gobies were present, which is widely viewed as a biological indication of ecosystem integrity (Senanayake and Moyle, 1982; Brasher *et al.*, 2006; Blum *et al.*, 2014). Furthermore, with few exceptions, all invasion hotspots on Kaua'i, Maui, and Hawai'i corresponded to native biodiversity hotspots or watersheds harbouring relatively diverse complements of native species (*i.e.* > 10 species; Fig. 2). This suggests that the same set of factors governs the dispersal, establishment, and coexistence of aquatic fauna in Hawaiian streams, regardless of provenance (Planty-Tabacchi *et al.*, 1996; Levine and D'Antonio, 1999; Stohlgren *et al.*, 1999). This inference is consistent with evidence from plant communities suggesting that ecosystem productivity is associated with high native species diversity and invasibility (Hooper *et al.*, 2005; Tilman *et al.*, 2012), as well as evidence that water quality and hydrology mediate habitability of Hawaiian streams for fishes and invertebrates (Fitzsimons *et al.*, 1997; McIntosh *et al.*, 2002; Brasher, 2003; Walter *et al.*, 2012; Blum *et al.*, 2014).

We detected some notable departures from broad, archipelago-wide patterns of aquatic community biodiversity that further illustrate native aquatic biodiversity alone does not predict invasion potential. For example, nine out of nineteen invasion hotspots on O'ahu were not concordant with native biodiversity hotspots, and seven of the nine invasion hotspots corresponded to watersheds with high human population density (> 230 person/km^2). This raises the possibility that invasion hotspots may result from factors like ecological feedbacks that originate from non-native species engineering conditions that directly or indirectly constrain native species (Didham *et al.*, 2005). Introduced poeciliids and armoured loricariid catfish, for example, compete with native species for food resources and shift nutrient availability (Capps and Flecker, 2013; Holitzki *et al.*, 2013). Ecological feedbacks might be exacerbated in watersheds that support greater human population densities, like those on O'ahu, and may become more prevalent as human habitation continues to rise across the Hawaiian archipelago. Mesocosm or field-scale manipulative experiments could illustrate the extent to which invasion hotspots arise due to ecological feedbacks that constrain native species (Gurevitch and Padilla, 2004).

It is important to note that we cannot exclude the possibility that the observed relationships between non-native and native species richness are in some way a product of variation in sampling effort. Consistent with the statistics of encounter probabilities, more records of species occurrences are available for more extensively-surveyed streams compared to less-surveyed streams (Fig. 1). After exploring other methods to constrain the influence of observation intensity, we accounted for differential sampling effort by incorporating the number of surveys per watersheds as a covariate in all statistical analyses. Regardless of the approach taken,

we nonetheless found that human demography and land-use were predictors of non-native species richness and native species richness, respectively. Thus, we consider it unlikely that the observed relationships between non-native and native species richness is a sampling artifact. Similarly, it is also unlikely that the concordance of invasion and native biodiversity hotspots is a sampling artifact. It is also notable that, despite differences in observation intensity, consistent patterns (*i.e.* in the location of hotspots) were found for all four major taxonomic groups. This further suggests that sampling effort, while important, exerted less influence than biotic and abiotic factors governing stream biodiversity in Hawai'i.

Archival data like those utilized here are valuable but imperfect resources for studying patterns of biological invasions of oceanic island streams. Some limitations warrant careful consideration. For example, dates may not be available for all survey records. Consequently, archives offer cumulative perspectives, as opposed to contemporary perspectives, on species introductions. This can result in misleading inferences of species distributions (Blum *et al.*, 2014), and complicate comparisons to other factors of interest (*e.g.* human population density, indicators of stream impairment) that may vary over time. Addressing this limitation would increase the power of data-driven approaches to oceanic island freshwater conservation and management. Analyses of survey records also must account for the possibility of spatial autocorrelation because the presence or absence of a species can depend on site proximity within a watershed and the confluence of nearby watersheds. Though still present, the potential for spatial autocorrelation is lower across oceanic island archipelagos like the Hawaiian Islands, where nearly all watersheds are discrete hydrological units (*i.e.* that only connect by way of inhospitable marine environments). The distinctiveness and heterogeneity of oceanic island watersheds are well illustrated across the Hawaiian archipelago, where watersheds on different islands at times are more similar to one another than are neighbouring watersheds (Moody *et al.*, 2015). Nonetheless, further understanding of freshwater biodiversity could be improved by accounting for the potential influence of proximity on watershed attributes and habitation.

In aggregate, the diversity of oceanic island streams has been increasing worldwide with the establishment and accumulation of non-native species. Freshwater fish diversity, for example, has increased dramatically on Pacific islands (McDowall, 1990; McDowall *et al.*, 2001; Nico and Walsh, 2011) including those in the Hawaiian archipelago (Eldredge and Miller, 1995; Eldredge, 2000; Yamamoto and Tagawa, 2000; Blum *et al.*, 2014). Though higher biodiversity is often considered to be a favourable condition, elevated diversity on oceanic islands can be a sign of extirpation or loss of native species (Sax and Gaines, 2008). The observed relationships between native and non-native species richness indicate that ecological saturation has not been achieved in streams across the Hawaiian archipelago (Fig. 5), which suggests that stream faunal diversity is constrained more so by geographic isolation than by limited ecological resources. Though the functional diversity of non-native species in Hawaiian streams might suggest otherwise (Annexe 2), our findings indicate that ecological niches remain open and available. Thus Hawaiian streams likely remain vulnerable to further invasion.

Our findings offer further affirmation of long-standing recommendations that control and mitigation of non-native species could promote conservation of native species on oceanic islands (Brasher, 2003; Nico and Walsh, 2011; Walter *et al.*, 2012; Blum *et al.*, 2014). Though lessons likely can be learned from the conservation and management of terrestrial ecosystems (Hadfield *et al.*, 1993; Loope *et al.*, 2001; Benning *et al.*, 2002; Boyer, 2008), formulating strategies to ward off extirpation of native species in oceanic island streams warrants more careful study. Manipulative experiments (*e.g.* removals) could clarify the functional diversity and influence of invasive species on vital ecosystem processes like nutrient cycling, and thus afford further perspective on niche partitioning, trophic structure, and ecological saturation of oceanic island streams. Inferences based on archives like the DAR Atlas also could be strengthened by conducting regular, archipelago-wide quantitative surveys to analyze hierarchical (*i.e.* within and across islands) variation in species richness and to estimate relative abundance (Blum *et al.*, 2014). Since costs are often a barrier, we advocate use of technologically simple approaches (*e.g.* snorkel surveys) that yield reliable data on community composition (Higashi and Nishimoto, 2007) as well as demographic processes that can determine the likelihood of species persistence (Hain *et al.*, 2016). However, incorporating emerging technologies, like environmental DNA, could further understanding of occurrence and abundance at little additional cost (Ficetola *et al.*, 2008; Jerde *et al.*, 2011). This could clarify the nature of source-sink dynamics within and across islands- especially for migratory species like amphidromous fishes and invertebrates- and thus offer guidance on managing areas harbouring populations on the brink of extirpation or that disproportionately sustain the well-being of populations elsewhere in the archipelago. Integrative analyses that incorporate additional environmental data (*e.g.* on water quality, commercial transport pathways, land development) also could help guide implementation of precautionary steps aimed at reducing the likelihood of future introductions.

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REFERENCES

ABELL R., THIEME M.L. & REVENGA C. *et al*. [28 authors], 2008. - Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *Bioscience*, 58: 402-414.

ALDA F., GAGNE R.B., WALTER R.P., HOGAN J.D., MOODY K.N., ZINK F., MCINTYRE P.B., GILLIAM J.F. & BLUM M.J., 2016. - Colonization and demographic expansion of freshwater fauna across the Hawaiian Archipelago. *J. Evol. Biol*., 29: 2054-2069.

AMADON D., 1950. - The Hawaiian honeycreepers (Aves, Drepaniidae). *Bull. Am. Mus. Nat. Hist*., 95: 157-268.

ASNER G.P., KNAPP D.E., KENNEDY-BOWDOIN T., JONES M.O., MARTIN R.E., BOARDMAN J. & HUGHES R.F., 2008. - Invasive species detection in Hawaiian rainforests using airborne imaging spectroscopy and LiDAR. *Remote Sens. Environ*., 112: 1942-1955.

ATHENS J.S., 2009. - *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. *Biol. Invasions*, 11: 1489.

BENNING T.L., LAPOINTE D., ATKINSON C.T. & VITOUSEK P.M., 2002. - Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. *Proc. Natl. Acad. Sci.,* 99: 14246-14249.

BLACKBURN T.M., CASSEY P., DUNCAN R.P., EVANS K.L. & GASTON K.J., 2004. - Avian extinction and mammalian introductions on oceanic islands. *Science*, 305: 1955-1958.

BLOB R.W., BRIDGES W.C., PTACEK M.B., MAIE T., CEDIEL R.A., BERTOLAS M.M., JULIUS M.L. & SCHOENFUSS H.L., 2008. - Morphological selection in and extreme flow environment: body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*. *Int. Comp. Biol.,* 48: 734-749.; (Erratum) 49: 732-734 (2009).

BLOB R.W., KAWANO S.M., MOODY K.N., BRIDGES W.C., MAIE T., PTACEK M.B. & SCHOENFUSS H.L., 2010. - Morphological selection and the evaluation of potential tradeoffs between escape from predators and the climbing of waterfalls in the Hawaiian stream goby *Sicyopterus stimpsoni*. *Integr. Comp. Biol*., 50: 1185-1199.

BLUM M.J., GILLIAM J.F. & MCINTYRE P.B., 2014. - Development and use of genetic methods for assessing aquatic environmental condition and recruitment dynamics of native stream fishes on Pacific islands. SERDP Final Report RC-1646.

BOYER A.G., 2008. - Extinction patterns in the avifauna of the Hawaiian Islands. *Divers. Distrib*., 14: 509-517.

BRASHER A.M.D., 1996. - Monitoring the Distribution and Abundance of Native Gobies (Oopu) in Waikolu and Pelekunu Streams on the Island of 0Molokai. Honolulu: Cooperative National Park Resources Studies Unit. Technical Report no. 113.

BRASHER A.M.D., 2003. - Impacts of human disturbances in biotic communities in Hawaiian streams. *Bioscience*, 53: 1052-1060.

BRASHER A.M.D., WOLLF R.H. & LUNTON C.D., 2004. - Associations among land use, habitat characteristics, and invertebrate community structure in nine streams on the island of Oahu, Hawaii, 1999-2001. No. 3-4256. Reston, Virginia: US Geological Survey, 2004.

BRASHER A.M., LUTON C.D., GOODBRED S.L. & WOLFF R.H., 2006. - Invasion patterns along elevation and urbanization gradients in Hawaiian streams. *Trans. Am. Fish. Soc*., 135: 1109-1129.

BROWN L.R., 2000. - Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environ. Biol. Fish*., 57: 251-269.

BRYAN W.A., 1915. - Natural History of Hawaii: Being an Account of the Hawaiian People, the Geology and Geography of the Islands, and the Native and Introduced Plants and Animals of the Group. 596 p. Honolulu Hawai'i: The Hawaiian Gazette Co., Ltd.

BUTCHART S.H., WALPOLE M., COLLEN B. *et al*. [11 authors], 2010. - Global biodiversity: indicators of recent declines. *Science*, 328: 1164-1168.

CAMBRAY J.A., 2003. - Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. *Hydrobiology*, 500(1): 217-230.

CAPPS K.A. & FLECKER A.S., 2013. - Invasive aquarium fish transform ecosystem nutrient dynamics. *Proc. R. Soc. Lond. B*, 280(1769): 20131520.

CARR G.D. & KYHOS D.W., 1981. - Adaptive radiation in the Hawaiian silversword alliance (Compositae: Madiinae). I. Cyotgenetics of spontaneous hybrids. *Evolution*, 35: 543-556.

CARSON H.L. & KANESHIRO K.Y., 1976. - Drosophila of Hawai'i: systematics and ecological genetics. *Annu. Rev. Ecol. Syst*., 7: 311-346.

CHAPIN III F.S., ZAVALETA E.S., EVINER V.T. *et al*. [11 authors], 2000. - Consequences of changing biodiversity. *Nature*, 405: 234-242.

CHARLES H. & DUKES J.S., 2008. - Impacts of invasive species on ecosystem services. *In*: Biological Invasions, Ecological Series 193 (Nentwig W., ed.), pp. 217-237. Berlin Heidelberg: Springer-Verlag

CINCOTTA R.P., WISNEWSKI J. & ENGELMAN R., 2000. - Human population in the biodiversity hotspots. *Nature*, 404: 990-992.

CORNELL H.V. & LAWTON J.H., 1992. - Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *J. Anim. Ecol*., 1992: 1-12.

D'ANTONIO C.M. & DUDLEY T.L., 1995. - Biological invasions as agents of change on islands versus mainlands. *In*: Islands, Ecological series 115 (Vitousek *et al*., eds), pp. 103-121. Berlin Heidelberg: Springer-Verlag.

DIDHAM R.K., TYLIANAKIS J.M., HUTCHISON M.A., EWERS R.M. & GEMMELL N.J., 2005. - Are invasive species the drivers of ecological change? *Trends Ecol. Evol*., 20*:* 470-474.

DRAKE J.M. & LODGE D.M., 2004. - Global hot spots of biological invasions: evaluating options for ballast–water management. *Proc. R. Soc. Lond. B,* 271: 575-580.

EL-SABAAWI R.W., FRAUENDOR T.C., MARQUES P.S., MACKENZIE R.A., MANNA L.R., MAZZONI R., PHILLIP D.A., WARBANSKI M.L. & ZANDONÀ E., 2016. - Biodiversity and ecosystem risks arising from using guppies to control mosquitoes. *Biol. Lett*., 12: 20160590.

ELDREDGE L.G. (ed.), 2000. - Non-Indigenous Freshwater Fishes, Amphibians and Crustaceans of the Pacific and Hawaiian Islands. Invasive Species in the Pacific: A Technical Review and Draft Regional Strategy. 197 p. South Pacific Regional Environment Programme.

ELDREDGE L.G. & MILLER S.E., 1995. - How many species are there in Hawaii? *Bishop Mus. Occ. Pap.,* 41: 3-17.

ELTON C.S., 1958. - The Ecology of Invasions by Animals and Plants. 196 p. London, UK: Methuen.

ENGLUND R.A., 1999. - The impacts of introduced poeciliid fish and Odonata on the endemic *Megalagrion* (Odonata) damselflies of Oahu Island, Hawaii. *J. Insect Conserv.*, 3: 225-243.

ESRI, 2016. - ArcGIS Desktop: Release 10.3.1. Redlands, CA: Copyright 2016 Environmental Systems Research Institute, Inc.

FAUSCH K.D., TORGERSE C.E., BAXTER C.V. & LI H.W., 2002. - Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes: a continuous view of the river is needed to understand how processes interacting among scales set the context for stream fishes and their habitat. *BioScience*, 52: 483-498.

FICETOLA G.F., MIAUD C., POMPANON F. & TABERLET P., 2008. - Species detection using environmental DNA from water samples. *Biol. Lett.*, 4: 423-425.

FITZSIMONS J.M., ZINK R.M. & NISHIMOTO R.T., 1990. - Genetic variation in the Hawaiian stream goby, *Lentipes concolor*. *Biochem. Syst. Ecol.*, 18: 81-83.

FITZSIMONS J.M., SCHOENFUSS H.L. & SCHOENFUSS T.C., 1997. - Significance of unimpeded flows in limiting the transmission of parasites from exotics to Hawaiian stream fishes. *Microensia*, 30: 117-125.

FONT W.F., 2003. - The global spread of parasites: what do Hawaiian streams tell us? *BioScience*, 53: 1061-1067.

FOX M.D. & FOX B.J., 1986. - The susceptibility of natural communities to invasion. *In*: Ecology of Biological Invasions (Groves R.H. & Burdon J.J., eds), pp. 57-60. Cambridge, UK: Univ. Press.

FULTON W., PENDALL R., NGUYEN M. & HARRISON A., 2001. - Who Sprawls Most? How Growth Patterns Differ across the U.S. Center on Urban and Metropolitan Policy. 24 p. Washington, D.C.: The Brookings Institute Center on Urban and Metropolitan Policy.

GAGNE R.B., HOGAN J.D., PRACHEIL B.M., MCINTYRE P.B., HAIN E.F., GILLIIAM J.F. & BLUM M.J., 2015. - Spread of an introduced parasite across the Hawaiian archipelago independent of its introduce host. *Freshw. Biol.,* 60: 311-322.

GAGNE R.B., HEINS D.C., MCINTYRE P.B., GILLIAM J.F. & BLUM M.J., 2016. - Mutual dilution of infection by an introduced parasite in native and non-native stream fishes across Hawaii. *Parasitology*: 1-10.

GASTON K.J., JONES A.G., HÄNEL C. & CHOWN S.L., 2003. - Rates of species introduction to a remote oceanic island. *Proc. R. Soc. B-Biol. Sci.*, 270: 1091-1098.

GILLESPIE R.G., CLARIDGE E.M. & RODERICK G.K., 2008. - Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Mol. Ecol.*, 17: 45-57.

GOTELLI N.J. & COLWELL R.K., 2001. - Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4: 379-391.

GUREVITCH J. & PADILLA D.K., 2004. - Are invasive species a major cause of extinctions? *Trends Ecol. Evol.*, 19: 470-474.

HADFIELD M.G., MILLER S.E. & CARWILE A.H., 1993. - The decimation of endemic Hawai'ian tree snails by alien predators. *Am. Zool.*, 33: 610-622.

HAIN E.F., LAMPHERE B.A., BLUM M.J., MCINTYRE P.B., NELSON S.A. & GILLIAM J.F., 2016. - Comparison of Visual Survey and Mark–Recapture Population Estimates of a Benthic Fish in Hawaii. *Trans. Am. Fish. Soc.*, 145: 878-887.

HIGASHI G.R. & YAMAMATO M.N., 1993. - Rediscovery of "extinct" *Lentipes concolor* (Pisces: Gobiidae) on the island of Oahu, Hawaii. *Pac. Sci.*, 47: 115-117.

HIGASHI G.R. & NISHIMOTO R.T., 2007. - The point quadrat method: a rapid assessment of Hawaiian streams. *Bishop Mus. Bull. Cult. Environ. Stud.*, 3: 305-313.

HOGAN J.D., BLUM M.J., GILLIAM J.F., BICKFORD N. & MCINTYRE P.B., 2014. - Consequences of alternative dispersal strategies in a putatively amphidromous fish. *Ecology*, 95: 2397-2408.

HOLITZKI T.M., MACKENZIE R.A. WIEGNER T.N. & MCDERMID K.J., 2013. - Differences in ecological structure, function, and native species abundance between native and invaded Hawaiian streams. *Ecol. Appl.*, 23: 1367-1383.

HOOPER D.U., CHAPIN F.S., EWEL J.J. *et al.* [11 authors], 2005. - Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75: 3-35.

HUBBELL S.P., 2001. - The Unified Neutral Theory of Biodiversity and Biogeography. 293 p. Princeton: Princeton Univ. Press.

JERDE C.L., MAHON A.R., CHADDERTON W.L. & LODGE D.M., 2011. - "Sight-unseen" detection of rare aquatic species using environmental DNA. *Conserv. Lett.*, 4: 150-157.

KENNEDY T.A., NAEEM S., HOWE K.M., KNOPS J.M., TILMAN D. & REICH P., 2002. - Biodiversity as a barrier to ecological invasion. *Nature*, 417: 636-638.

KIDO M.H., 1996. - Diet and food selection in the endemic Hawaiian amphidromous goby, *Sicyopterus stimpsoni* (Pisces: Gobiidae). *Environ. Biol. Fish*, 45: 199-209.

KIER G., KREFT H., LEE T.M., JETZ W., IBISCH P.L., NOWICKI C., MUTKE J. & BARTHLOTT W., 2009. - A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci.*, 106: 9322-9327.

KLASNER F. & MIKAMI C.D., 2003. - Land Use on the Island of Oahu, 1998. 20 p. U.S. Geological Survey, Water Resources Investigations, Report 02-4301, Honolulu, Hawaii.

LEGENDRE P., 2008. - Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.*, 1: 3-8.

LEPRIEUR F., BEAUCHARD O., BLANCHET S., OBERDOFF T. & BROSSE S., 2008. - Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biol.*, 6: e28.

LEVIN D.A., FRANCISCO-ORTEGA J. & JANSEN R.K., 1996. - Hybridization and the extinction of rare plant species. *Conserv. Biol.*, 10: 10-16.

LEVINE J. & D'ANTONIO C.M., 1999. - Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87: 15-26.

LINDSTROM D.P., BLUM M.J., WALTER R.P., GAGNE R.B. & GILLIAM J.F., 2012. - Molecular and morphological evidence of distinct evolutionary lineages of *Awaous guamensis* in Hawai'i and Guam. *Copeia*, 2: 293-300.

LOCKWOOD J.L., CASSEY P. & BLACKBURN T., 2005. - The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.*, 20: 223-228.

LOOPE L.L., HOWARTH F.G., KRAUS F. & PRATT T.K., 2001. - Newly emergent and future threats of alien species to Pacific birds and ecosystems. *Stud. Avian Biol.,* 22: 291-304.

LYONS K.G. & SCHWARTZ M.W., 2001. - Rare species loss alters ecosystem function–invasion resistance. *Ecol. Lett.,* 4: 358-365.

MACARTHUR R.H. & WILSON E.O., 1963. - Equilibrium theory of insular zoogeography. *Evolution*, 17: 373-387.

MACARTHUR R.H. & WILSON E.O., 1967. - The Theory of Island Biogeography. 222 p. Princeton: Princeton Univ. Press.

MAIE T., SCHOENFUSS H.L & BLOB R.W., 2012. - Performance and scaling of a novel locomotor structure: adhesive capacity of climbing gobiid fishes. *J. Exp. Biol.*, 215: 3925-3936.

MARCHETTI M.P., LIGHT T., MOYLE P.B. & VIERS J.H., 2004. - Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecol. Appl.*, 14: 1507-1525.

MCDOWALL R.M., 1990. - New Zealand Freshwater Fishes - A Natural History and Guide (2nd edit.). 233 p. Auckland: Heinemann Reed.

MCDOWALL R.M., 2003. - Hawaiian biogeography and the islands' freshwater fish fauna. *J. Biogeogr.*, 30: 703-710.

MCDOWALL R.M., 2004. - Ancestry and amphidromy in island freshwater fish faunas. *Fish Fish.*, 5: 75-85.

MCDOWALL R.M., 2010. - Why be amphidromous: expatrial dispersal and the place of source sink population dynamics? *Rev. Fish Biol. Fish.*, 20: 87-100.

MCDOWALL R.M., ALLIBONE R.M. & CHADDERTON W.L., 2001. - Issues for the conservation and management of Falkland Islands freshwater fishes. *Aquat. Conserv. Mar. Freshw. Ecosyst.*, 11: 473-486.

MCINTOSH M.D., BENBOW M.E. & BURKY A.J., 2002. - Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Res. Appl.*, 18: 569-581.

MCKINNEY M.L., 2002. - Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Global Ecol. Biogeogr.,* 11: 343-348.

MEADOR M.R., BROWN L.R. & SHORT T., 2003. - Relations between introduced fish and environmental conditions at large geographic scales. *Ecol. Indic.*, 3: 81-92.

MITCHELL A.L. & KNOUFT J.H., 2009. - Non-native fishes and native species diversity in freshwater fish assemblages across the United States. *Biol. Invasions*, 11: 1441-1450.

MOODY K.N., HUNTER S.N., CHILDRESS M.J., BLOB R.W., SCHOENFUSS H.L., BLUM M.J. & PTACEK M.B., 2015. - Local adaptation despite high gene flow in the waterfall-climbing Hawaiian goby, *Sicyopterus stimpsoni*. *Mol. Ecol.,* 24: 545-563.

MOODY K.N., KAWANO S.M., BRIDGES W.C., BLOB R.W., SCHOENFUSS H.L & PTACEK M.B., 2017. - Contrasting post-settlement selection results in many-to-one mapping of high performance phenotypes in the Hawaiian waterfall-climbing goby *Sicyopterus stimpsoni*. *Evol. Ecol.,* 1-28.

MOONEY H.A. & CLELAND E.E., 2001. - The evolutionary impact of invasive species. *P. Natl. Acad. Sci.*, 98*:* 5446-5451.

MOYLE P.B. & LIGHT T., 1996. - Fish invasions in California: do abiotic factors determine success? *Ecology,* 77: 1666-670.

MYERS N., 1988. - Threatened biotas: "Hotspots" in tropic forests. *Environmentalist*, 8: 187-208.

MYERS N., MITTERMEIER R.A., MITTERMEIER C.G., DA FONSECA G.A. & KENT J., 2000. - Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.

NAEEM S., DUFFY J.E. & ZAVALETA E., 2012. - The functions of biological diversity in an age of extinction. *Science*, 336: 1401-1406.

NICO L.G. & WALSH S.J., 2011. - Non-indigenous freshwater fishes on tropical Pacific islands: a review of eradication efforts. *In*: Island Invasives: Eradication and Management. Proc. of the Int. Conf. on Island Invasives (Veitch C.R., Clout M.N. & Towns D.R., eds), pp. 97-107. Switzerland: IUCN.

O'DOWD D.J., GREEN P.T. & LAKE P.S., 2003. - Invasional 'meltdown' on an oceanic island. *Ecol. Lett.,* 6*:* 812-817.

OKI D.S. & BRASHER A.M.D., 2003. - Environmental setting and implications for water quality and Aquatic Biota, Oahu, Hawaii. 98 p. U.S. Geological Survey, Water Resources Investigations, Report 03-4156, Honolulu, Hawaii.

OKSANEN J., BLANCHET F.G., FRIENDLY M. *et al.* [13 authors], 2016. - vegan: Community ecology package. R package version 2.4-1. https://CRAN.R-project.org/package=vegan

PAULAY G. & MEYER C., 2002. - Diversification in the tropical Pacific: comparisons between marine and terrestrial systems and the importance of founder speciation. *Integ. Comp. Biol.*, 42: 922-934.

PERES-NETO P.R. & LEGENDRE P., 2010. - Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecol. Biogeogr.*, 19: 174-184.

PLANTY-TABACCHI A.M., TABACCHI E., NAIMAN R.J., DEFERRARI C. & DECAMPS H., 1996. - Invasibility of species-rich communities in riparian zones. *Conserv. Biol.*, 10: 598-607.

POLHEMUS D.A., 1993. - Damsels in distress: a review of the conservation status of Hawaiian *Megalagrion* damselflies (Odonata: Coenagrionidae). *Aquat. Conserv.,* 3: 343-349.

POLHEMUS D.A. & ASQUITH A., 1996. - Hawaiian Damselflies: A Field Identification Guide. 122 p. Honolulu: Bishop Museum Press.

PRENTER J., MACNEIL C., DICK J.T.A. & DUNN A.M., 2004. - Role of parasites in animal invasion. *Trends Ecol. Evol.*, 19: 385-390.

PRINGLE C.M. & RAMIREZ A., 1998. - Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Freshw. Biol.*, 39: 359-373.

R CORE TEAM, 2014. - R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

RAO C.R., 1964. - The use and interpretation of principal component analysis in applied research. *Sankhya: Indian J. Stat., Ser. A*, 26: 329-358.

RESH V.H., BARNES J.R., BENIS-STEGER B. & CRAIG D.A., 1992. - Life history features of some macroinvertebrates in a French Polynesia stream. *Stud. Neotrop. Fauna E*, 27: 145-153.

RICCIARDI A. & MACISAAC H.J., 2010. - Impacts of biological invasions on freshwater ecosystems. *In*: Fifty Years of Invasion Ecology: The Legacy of Charles Elton (Richardon D.M., ed.), pp. 211-224. Oxford, UK: Wiley-Blackwell.

SALA O.E., CHAPIN F.S., ARMESTO J.J. *et al.* [11 authors], 2000. - Global biodiversity scenarios for the year 2100. *Science*, 287: 1770-1774.

SAVIDGE J.A., 1987. - Extinction of an island forest avifauna by an introduced snake. *Ecology*, 68: 660-668.

SAX D.F. & BROWN J.H., 2000. - The paradox of invasion. *Global Ecol. Biogeogr.*, 9: 363-371.

SAX D.F. & GAINES S.D., 2008. - Species invasions and extinction: The future of native biodiversity on islands. *Proc. Natl. Acad. Sci.*, 105: 11490-11497.

SAX D.F., GAINES S.D. & BROWN J.H., 2002. - Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.*, 160: 766-783.

SCHLOSSER I.J., 1991. - Stream fish ecology: a landscape perspective. *BioScience*, 41: 704-712.

SCOTT M.C. & HELFMAN G.S., 2001. - Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries*, 26: 6-15.

SCRUCCA L., 2012. - Dispmod: dispersion models R package version 11. http://CRANR-projectorg/package=dispmod.

SENANAYAKE F.R. & MOYLE P.B., 1982. - Conservation of freshwater fishes of Sri Lanka. *Biol. Conserv.*, 22: 181-195.

SIMBERLOFF D., 1995. - Why do introduced species appear to devastate islands more than mainland areas? *Pac. Sci.*, 49: 87-97.

SIMBERLOFF D., 2006. - Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.*, 9: 912-919.

SIMBERLOFF D. & VON HOLLE B., 1999. - Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions*, 1: 21-32.

SIMBERLOFF D. & WILSON E.O., 1969. - Experimental zoogeogrpahy of islands: The colonization of empty islands. *Ecology*, 50: 278-296.

STACHOWICZ J.J. & TILMAN D., 2005. - What species invasions tell us about the relationship between community saturation, species diversity and ecosystem functioning. *In*: Species Invasions: Insights into Ecology, Evolution and Biogeography (Sax D., Stachowicz J. & Gaines S., eds), pp. 41-64. Sinauer, Sunderland MA.

STACHOWICZ J.J., WHITLATCH R.B. & OSMAN R.W., 1999. - Species diversity and invasion resistance in a marine ecosystem. *Science*, 286: 1577-1579.

STOHLGREN T.J., BINKLEY D., CHONG G.W., KALKHAN M.A., SCHELL L.D., BULL K.A., OTSUKI Y., NEWMAN G., BASHKIN M. & SON Y., 1999. - Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69: 25-46.

TILMAN D., 1997. - Distinguishing between the effects of species diversity and species composition. *Oikos*, 80: 185.

TILMAN D., REICH P.B. & ISBELL F., 2012. - Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci.*, 109: 10394-10397.

TORGERSEN C.E., GRESSWELL R.E., BATEMAN D.S. & BURNETT K.M., 2008. - Spatial identification of tributary impacts in river networks. *In*: River Confluences, Tributaries and the Fluvial Network (Rice S.P., Roy A.G., Rhoads B.L., eds), pp. 159-181. Chichester, UK: John Wiley & Sons Ltd.

VAN RIPPER C., VAN RIPPER S.G., GOFF M.L. & LAIRD M., 1986. - The epizzotiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.*, 56: 327-344.

VITOUSEK P.M., 1988. - Diversity and biological invasions of oceanic islands. *In*: Biodiversity (Wilson E.O. & Peter F.M., eds), pp. 181-189. Washington, D.C.: National Academic Press.

VITOUSEK P.M., D'ANTONIO C.M., LOOPE L.L., REJMANEK M. & WESTBROOKS R., 1997. - Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.*: 1-16.

WALTER R.P., HOGAN J.D., BLUM M.J., GAGNE R.B., HAIN E.F., GILLIAM J.F. & MCINTYRE P.B., 2012. - Climate change and conservation of endemic amphidromous fishes in Hawaiian streams. *Endangered Species Res.*, 16: 261-272.

WANG L., LYONS J., KANEHL P. & GATTI R., 1997. - Influences of watershed land-use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries*, 22: 6-12.

WARE C., BERGE J., SUNDET J.H., KIRKPATRICK J.B., COUTTS A.D., JELMERT A., STEFFEN M., OLSEN O.V., WISZ M.S. & ALSOS I.G., 2014. - Climate change, non-indigenous species and shipping: assessing the risk of species introduction to a high-Arctic archipelago. *Divers. Distrib.*, 20: 10-19.

WARNER R.E., 1968. - The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *The Condor*, 70: 101-120.

WHITTAKER R.J. & FERNÁNDEZ-PALACIOS J.M., 2007. - Island Biogeography: Ecology, Evolution, and Conservation. 2nd edit., 416 p. Oxford Univ. Press.

WILSON E.O., 1961. - The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.*, 95: 169-193.

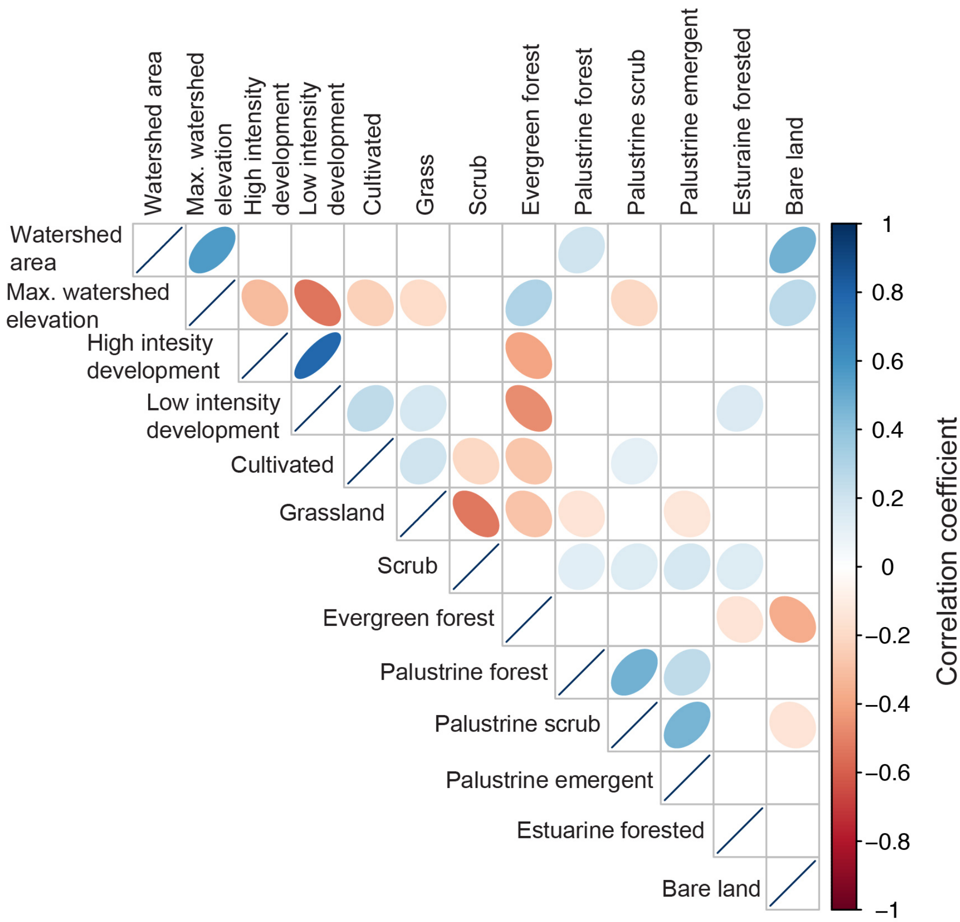
WYATT K.B., CAMPOS P.F., GIBLERT C.M.T, KOLOKOTRONIS S.O., HYENS W.H., DESALLE R., DASZAK P., DE MACPHEE R. & GREENWOO A.D, 2008. - Historical mammal extinction on Christmas Island (Indian Ocean) correlates with introduced infectious disease. *PloS ONE*, 3: e3602.

YAMAMOTO M.N. & TAGAWA A.W., 2000. - Hawai'i's Native and Exotic Freshwater Animals. 200 p. Hawai'i: Mutual Publishing.

ZIEGLER A.C., 2002. - Hawaiian Natural History, Ecology, and Evolution. 688 p. Hawai'i: Univ. of Hawaii Press.

ZIMMERMAN E.C., 1948. - Insects of Hawai'i. Vol.1, Introduction. 250 p. Hawai'i: Univ. of Hawai'i Press.

Annexe 1. – Correlation matrix of land-cover and watershed variables across all Hawaiian watersheds. Ellipses represent significant covariance between variables at $P < 0.05$, with negative correlation coefficients in warmer colours (red) and positive correlation coefficients in cooler cools (blue).



Annexe 2. – Hawaiian native and non-native species list for each taxonomic group.

Species name	Common name	Native/Nonnative	Taxonomic group
Awaous guamensis	o'opu nakea	Native	Fish
Eleotris sandwicensis	Hawaiian sleeper; 'o'opu akupa	Native	Fish
Lentipes concolor	o'opu alamo'o	Native	Fish
Stenogobius hawaiiensis	o'opu naniha	Native	Fish
Sicyopterus stimpsoni	o'opu nopili	Native	Fish
Amphilophus citinellus	midas cichlid	Non-native	Fish
Ancistrus temmincki	bristlenose catfish	Non-native	Fish
Archocentrus nigrofasciatus	convict cichlid	Non-native	Fish
Astronotus ocellatus	oscar	Non-native	Fish
Carassius auratus	goldfish	Non-native	Fish
Channa maculata	snakehead	Non-native	Fish
Cichlid sp.		Non-native	Fish
Clarius fuscus	Chinese catfish	Non-native	Fish
Colossoma macropomum	blackfin pacu	Non-native	Fish
Corydoras aeneus	bronze corydoras	Non-native	Fish
Ctenopharyngodon idella	grass carp	Non-native	Fish
Cyprinus carpio	common carp/koi	Non-native	Fish
Gambusia affinis	mosquitofish	Non-native	Fish
Hemichromis elongatus	banded jewel cichlid	Non-native	Fish
Hemichromis fasciatus	banded jewel cichlid	Non-native	Fish
Hypostomus watwata	armored catfish	Non-native	Fish
Hypsophrys nicaraguensis	Nicaragua cichlid	Non-native	Fish
Ictalurus punctatus	channel catfish	Non-native	Fish
Lepomis macrochirus	bluegill sunfish	Non-native	Fish
Limia vittata	Cuban molly	Non-native	Fish
Lutjanus fulvus	Johanni cichlid	Non-native	Fish
Melanochromis johanni	Johanni cichlid	Non-native	Fish
Micropterus dolumieu	smallmouth bass	Non-native	Fish
Micropterus salmoides	largemouth bass	Non-native	Fish
Misgurnus anguillicaudatus	dojo/loach	Non-native	Fish
Monopterus albus	swamp eel/rice paddy eel	Non-native	Fish
Oncorhynchus mykiss	rainbow trout	Non-native	Fish
Oreochromis mossambicus	tilapia	Non-native	Fish
Poecilia latipinna	sailfin molly	Non-native	Fish
Poecilia reticulata	guppy	Non-native	Fish
Poecilia sphenops	black molly	Non-native	Fish
Poecilia velifera	sailfin molly	Non-native	Fish
Pterygoplichthys multradiatus	long-fin armored catfish	Non-native	Fish
Sarotherodon melanotheron	blackchin tilapia	Non-native	Fish
Thorichthys meeki	firemouth cichlid	Non-native	Fish
Tilapia zilli	redbelly tilapia	Non-native	Fish
Xenentodon cancila	freshwater needlefish	Non-native	Fish
Xiphophorus helleri	green swordtail	Non-native	Fish
Xiphophorus maculatus	swordtail	Non-native	Fish
Clithon cariosus		Native	Mollusks
Ferrissia sharpi		Native	Mollusks
Erinna aulacospira		Native	Mollusks
Erinna newcombi	Newcomb's snail	Native	Mollusks
Neritina granosa	Hihiwai	Native	Mollusks
Neritina vespertina	Hapawai	Native	Mollusks

Annexe 2. – Continued.

Species name	Common name	Native/Nonnative	Taxonomic group
Corbicula fluminea	Asiatic freshwater clam	Non-native	Mollusks
Musculium partumieum	clam	Non-native	Mollusks
Pisidium sp.	pill clam	Non-native	Mollusks
Sphaerid sp.		Non-native	Mollusks
Cipangopaludina chinensis	Chinese mystery snail	Non-native	Mollusks
Euglandina rosea	Wolf snail	Non-native	Mollusks
Helisoma sp.	ramshorn snail	Non-native	Mollusks
Lymnaeid sp.	pond snail	Non-native	Mollusks
Lymnea sp.	pond snail	Non-native	Mollusks
Melanoides tuberculata	Malayan trumpet snail	Non-native	Mollusks
Oxychilus sp.	glass snail	Non-native	Mollusks
Physid sp.	freshwater snail	Non-native	Mollusks
Pila conica		Non-native	Mollusks
Planoribid duryi		Non-native	Mollusks
Pomacea bridgesii		Non-native	Mollusks
Pomacea canaliculata	apple snail	Non-native	Mollusks
Pomacea paludosa	Florida/Cuba apple snail	Non-native	Mollusks
Pseudosuccinea columella	American ribbed fluke snail	Non-native	Mollusks
Tarebia granifera	quilted melania	Non-native	Mollusks
Thiaria granifera	thiarid freshwater snail	Non-native	Mollusks
Amphipod		Native	Crustacean
Atyoida bisulcata	mountain opae	Native	Crustacean
Copepod sp.		Native	Crustacean
Macrobrachium grandimanus	Hawaiian prawn	Native	Crustacean
Caridina weberi		Non-native	Crustacean
Hyalella azteca	long-wrist shrimp	Non-native	Crustacean
Isopod sp.		Non-native	Crustacean
Macrobrachium lar	Tahitian prawn	Non-native	Crustacean
Macrobrachium rosenbergii	Malaysian prawn	Non-native	Crustacean
Neocaridina denticulata	grass shrimp	Non-native	Crustacean
Procambii clarkii	Louisiana crawfish	Non-native	Crustacean
Scylla serrata	Samoan crab	Non-native	Crustacean
Anax junius	blue dragonfly	Native	Insect
Anax strenus	dragonfly	Native	Insect
Brachydeutera hebes		Native	Insect
Campsicnemus bicoloripes	fly	Native	Insect
Campsicnemus brevipes	skating fly	Native	Insect
Campsicnemus calcaratus	fly	Native	Insect
Campsicnemus exiguus	fly	Native	Insect
Campsicnemus lepidochaites	fly	Native	Insect
Campsicnemus miritibialis	fly	Native	Insect
Campsicnemus nigricollis	fly	Native	Insect
Campsicnemus patellifer	fly	Native	Insect
Campsicnemus ridiculus	fly	Native	Insect
Campsicnemus tibialis	fly	Native	Insect
Calospectra hawaiiensis	chironomid	Native	Insect
Chironomus hawaiiensis	chironomid	Native	Insect
Clunio vagans	midge	Native	Insect
Dasyhelea digna	midge	Native	Insect
Dasyhelea hawaiiensis	midge	Native	Insect

Annexe 2. – Continued.

Species name	Common name	Native/Nonnative	Taxonomic group
Dasyhelea platychaeta	midge	Native	Insect
Dasyrhicnoessa insularis	fly	Native	Insect
Empidid sp.	dance fly	Native	Insect
Eurynogaster mediocris		Native	Insect
Eurynogaster minor		Native	Insect
Eurynogaster obscura		Native	Insect
Forcipomyia hardyi	midge	Native	Insect
Hemerodromia sp.	dance fly	Native	Insect
Hyposmocoma sp.	case-making hawaiian aquatic moth	Native	Insect
Limnoxenus sp.	beetle	Native	Insect
Limonia grimshawi	crane fly	Native	Insect
Limonia hawaiiensis	crane fly	Native	Insect
Limonia jacobus	crane fly	Native	Insect
Limonia kauaiensis	crane fly	Native	Insect
Limonia nigropolita	crane fly	Native	Insect
Limonia perkinsi	crane fly	Native	Insect
Limonia stygipennis	crane fly	Native	Insect
Limonia swezeyi	crane fly	Native	Insect
Limonia variabilis	crane fly	Native	Insect
Megalagrion adytum	Alakai Swamp damselfly	Native	Insect
Megalagrion blackburni	Balckburn’s Hawaiian damselfly	Native	Insect
Megalagrion calliphya	Beautiful Hawaiian damselfly	Native	Insect
Megalagrion eudytum	Frosty Hawaiian damselfly	Native	Insect
Megalagrion heterogamias	Kaua‘i Mountain damselfly	Native	Insect
Megalagrion hawaiiense	Maui Upland damselfly	Native	Insect
Megalagrion leptodemas	crimson Hawaiian damselfly	Native	Insect
Megalagrion mauka	damselfly	Native	Insect
Megalagrion nigrohamatum nigrolineatum	Blackline Hawaiian damselfly	Native	Insect
Megalagrion oahuense	O‘ahu damselfly	Native	Insect
Megalagrion oceanicum	Oceanic Hawaiian damselfly	Native	Insect
Megalagrion oresitrophum	Slender Kaua‘i damselfly	Native	Insect
Megalagrion orobates	Yellowface Kaua‘i damselfly	Native	Insect
Megalagrion pacificum	Pacific Hawaiian damselfly	Native	Insect
Megalagrion paludicola	Kaua‘i Bog damselfly	Native	Insect
Megalagrion vagabundum	Scarlet Kaua‘i damselfly	Native	Insect
Megalagrion williamsoni	Williamson’s Hawaiian damselfly	Native	Insect
Megalagrion xanthomelas	Orangeblack Hawaiian damselfly	Native	Insect
Microvelia vagans	hawaiian pond bug	Native	Insect
Nesogonia blackburni	Blackburn’s skinner	Native	Insect
Nesogonia insularis		Native	Insect
Orthocladius grimshawi	midge	Native	Insect
Paraliancalus metallicus	fly	Native	Insect
Procanace acuminata	beach fly	Native	Insect
Procanace bifurcata	beach fly	Native	Insect
Procanace confusa	beach fly	Native	Insect
Procanace constricta	beach fly	Native	Insect
Procanace nigroviridis	beach fly	Native	Insect
Procance quadrisetosa	beach fly	Native	Insect
Procanacae williamsi	beach fly	Native	Insect
Procanace wirthi	beach fly	Native	Insect

Annexe 2. – Continued.

Species name	Common name	Native/Nonnative	Taxonomic group
Pseudosmittia paraconjugata		Native	Insect
Rhantus pacificus	beetle	Native	Insect
Saldula exulans	Hawaiian saldid bug	Native	Insect
Saldula oahuense		Native	Insect
Saldula procellaris		Native	Insect
Scatella cilipes	Hawaiian shore fly	Native	Insect
Scatella clavipes	Hawaiian shore fly	Native	Insect
Scatella femoralis	Hawaiian shore fly	Native	Insect
Scatella fluvialis	Hawaiian shore fly	Native	Insect
Scatella hawaiiensis	Hawaiian shore fly	Native	Insect
Scatella kauaiensis	Hawaiian shore fly	Native	Insect
Scatella mauiensis	Hawaiian shore fly	Native	Insect
Scatella oahuense	Hawaiian shore fly	Native	Insect
Scatella sexnotata	Hawaiian shore fly	Native	Insect
Scatella warreni	Hawaiian shore fly	Native	Insect
Scatella williamsi	Hawaiian shore fly	Native	Insect
Sigmataneurum chalybeum		Native	Insect
Sigmataneurum englundi		Native	Insect
Sigmatineurum omega		Native	Insect
Telmatogeton abnormis	midge	Native	Insect
Telmatogeton hirtus		Native	Insect
Telmatogeton torrenticola		Native	Insect
Telmatogeton williamsi		Native	Insect
Thallassomy setosipennis		Native	Insect
Thambemyia acrosticalis		Native	Insect
Trichomyia hawaiiensis		Native	Insect
Achradocera arcuata	long-legged fly	Non-native	Insect
Aedes albopictus		Non-native	Insect
Aedes nocturnus		Non-native	Insect
Anopheles nigerrimus		Non-native	Insect
Atrichopogon jacobsoni		Non-native	Insect
Brachydeutera ibari		Non-native	Insect
Buenoa pallipes		Non-native	Insect
Caenodes nigropunctatus		Non-native	Insect
Canaceoides angulatus		Non-native	Insect
Cheumatopsyche analis		Non-native	Insect
Cheumatopsyche bicintus		Non-native	Insect
Cheumatopsyche pettit		Non-native	Insect
Chironomid larvae		Non-native	Insect
Chrystous longipalpus		Non-native	Insect
Clogmia albipunctata		Non-native	Insect
Condylostylus longicornis	fly	Non-native	Insect
Cricotopus bicinctus		Non-native	Insect
Crocothemis servilia	Scarlet skimmer	Non-native	Insect
Culex pervigilans		Non-native	Insect
Culicid *sp*.		Non-native	Insect
Deielia fasciata		Non-native	Insect
Discocernia mera		Non-native	Insect
Dixa longistyla		Non-native	Insect
Dolichopus exsul		Non-native	Insect

Annexe 2. – Continued.

Species name	Common name	Native/Nonnative	Taxonomic group
Donaceus sp.		Non-native	Insect
Enallagma civile	Familiar bluet damselfly	Non-native	Insect
Enochrus sayi	water scavenger beetle	Non-native	Insect
Ephemeroptera sp.		Non-native	Insect
Erioptera bicornifer		Non-native	Insect
Goeldichironomus holoprasinus		Non-native	Insect
Hydrellia tritici		Non-native	Insect
Hydroptila arctia		Non-native	Insect
Hydroptila potosina	caddisfly larvae	Non-native	Insect
Ischnura posita	fragile forktail damselfly	Non-native	Insect
Ischnura ramburi	Rambur's fortail damselfly	Non-native	Insect
Limonia advena		Non-native	Insect
Mesovelia amoena		Non-native	Insect
Mesovelia mulsanti		Non-native	Insect
Notonecta indica	back swimmer	Non-native	Insect
Ochthera circularis		Non-native	Insect
Orthemis ferruginea		Non-native	Insect
Oxythira maya		Non-native	Insect
Pantala flavescens	brown dragonfly	Non-native	Insect
Paraphrosylus		Non-native	Insect
Pelastoneurus lugubris		Non-native	Insect
Psorophora signipennis		Non-native	Insect
Psychoda sp.		Non-native	Insect
Rhantus gutticollis	diving beetle	Non-native	Insect
Scatella stagnalis		Non-native	Insect
Sepedon aenescens		Non-native	Insect
Simuliid sp.		Non-native	Insect
Syntormon flexible		Non-native	Insect
Tachytrechus angustipennis		Non-native	Insect
Telmatogeton japonicus		Non-native	Insect
Thinophilus hardyi		Non-native	Insect
Toxorhynchites amboinensis		Non-native	Insect
Tramea abdominalis	vermilian glider	Non-native	Insect
Tramea lacerata		Non-native	Insect
Trichoptera sp.		Non-native	Insect
Trichocorixa reticulata		Non-native	Insect
Tropisternus lateralis humeralis		Non-native	Insect
Tropisternus salsamentus		Non-native	Insect

Annexe 3. – Non-native and native species hotspots for all taxonomic groups across the Hawaiian archipelago.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
All non-native species	Kaua'i	Hanalei River	21019	7.18	1.49	3.74	All native species	Kaua'i	Kalihiwai River	21025	10.66	1.00	2.89
	Kaua'i	Kīlauea	21028	52.05	0.58	6.65		Kaua'i	Kulihaili	21029	73.50	–2.10	1.00
	Kaua'i	Pīla'a	21031	20.94	–0.72	1.51		Kaua'i	Kapa'a	22004	82.97	0.18	1.24
	Kaua'i	Kapa'a	22004	82.97	0.18	1.24		O'ahu	Kaipapa'u	31010	178.91	0.43	0.82
	Kaua'i	Wailua River	22008	46.60	1.03	1.58		O'ahu	Kaluanui	31013	32.40	0.66	0.78
	Kaua'i	Hanamā'ulu	22012	120.74	–1.95	1.06		O'ahu	Punalu'u	31016	36.35	1.10	1.28
	Kaua'i	Hulē'ia	22015	6.00	0.05	1.32		O'ahu	Waiāhole	32004	30.11	1.02	1.01
	Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84		O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19
	O'ahu	Kaluanui	31013	32.40	0.66	0.78		O'ahu	Nu'uanu	33009	2015.31	–1.87	0.46
	O'ahu	Punalu'u	31016	36.35	1.10	1.28		O'ahu	Waikele	34010	736.01	–2.16	0.06
	O'ahu	Kahana	31018	19.21	1.62	2.08		O'ahu	Anahulu	36008	30.79	0.27	0.16
	O'ahu	Hakipu'u	32001	52.14	0.55	1.58		Moloka'i	Pelekunu	41009	0.10	1.74	0.30
	O'ahu	Waiāhole	32004	30.11	1.02	1.01		Maui	Honokōhau	61011	3.68	2.18	0.35
	O'ahu	Kahalu'u	32007	620.50	–0.85	0.76		Maui	Makamakaole	62006	7.96	0.55	0.05
	O'ahu	He'eia	32008	462.99	–1.53	2.96		Maui	Pi'ina'au	64011	0.86	1.81	–1.57
	O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19		Maui	Wailua Iki West	64015	0.94	2.26	–0.72
	O'ahu	Kāwā	32011	1157.72	–2.98	1.01		Maui	Waiohue	64018	0.57	1.79	–0.40
	O'ahu	Kawainui	32013	290.27	–0.48	6.46		Maui	Hanawī	64022	0.75	1.96	–1.60
	O'ahu	Waimānalo	32015	234.00	–1.48	0.19		Maui	Makapipi	64023	4.64	2.15	–0.86
	O'ahu	Nu'uanu	33009	2015.31	–1.87	0.46		Maui	Pua'alu'u Gulch	65012	1.23	–0.23	–0.47
	O'ahu	Moanalua	33012	440.75	–1.46	0.47		Maui	'Ohe'o Gulch	65013	0.78	1.70	–0.76
	O'ahu	Waiawa	34006	368.89	–0.95	0.14		Hawai'i	Waimanu	81035	0.22	1.99	2.21
	O'ahu	Waikele	34010	736.01	–2.16	0.06		Hawai'i	Wailoa	81044	6.83	1.36	–0.41
	O'ahu	Mākaha	35007	400.12	–0.42	0.32		Hawai'i	Nānue	82027	0.42	1.62	–2.18
	O'ahu	Ki'iki'i	36006	268.64	–0.73	0.18		Hawai'i	'Uma'uma	82030	1.10	1.66	–1.99
	O'ahu	Paukauila	36007	37.88	0.04	–0.09		Hawai'i	Mākea	82038	14.13	–2.18	–0.46
	O'ahu	Anahulu	36008	30.79	0.27	0.16		Hawai'i	Wai'a'ama	82042	37.10	–0.11	–0.47
	Maui	Wailua Iki West	64015	0.94	2.26	–0.72		Hawai'i	Kawainui	82043	1.87	0.74	–0.94
	Hawai'i	Waikōloa	81051	1.86	–0.33	–0.86		Hawai'i	Onomea	82044	27.32	–2.73	–0.57
	Hawai'i	Nānue	82027	0.42	1.62	–2.18		Hawai'i	Alakahi	82045	19.59	–2.27	–0.47
	Hawai'i	'Uma'uma	82030	1.10	1.66	–1.99		Hawai'i	Hanawī	82046	2.59	0.75	–0.71
	Hawai'i	Kawainui	82043	1.87	0.74	–0.94		Hawai'i	Ka'ie'ie	82049	29.54	–0.12	–0.86
	Hawai'i	Ka'ie'ie	82049	29.54	–0.12	–0.86		Hawai'i	Kapu'e	82053	13.24	1.04	–0.96
	Hawai'i	Honoli'i	82056	7.79	1.27	–0.90		Hawai'i	Pāhoehoe	82054	3.98	1.05	–0.72
	Hawai'i	Pūkīhae	82059	64.90	0.07	–0.74		Hawai'i	Pauka'a	82055	101.29	–4.46	–0.26
	Hawai'i	Wailuku	82060	7.91	1.67	–2.32		Hawai'i	Honoli'i	82056	7.79	1.27	–0.90
	Hawai'i	Wai'ula'ula	85003	35.49	–0.02	–2.44		Hawai'i	Wailuku	82060	7.91	1.67	–2.32

Annexe 3. – Continued.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
Non-native fishes	Kaua'i	Pīla'a	21031	20.94	–0.72	1.51	Native fishes	Kaua'i	Kalalau	21004	0.37	1.37	0.63
	Kaua'i	Kapa'a	22004	82.97	0.18	1.24		Kaua'i	Limahuli	21012	16.11	1.11	0.81
	Kaua'i	Wailua River	22008	46.60	1.03	1.58		Kaua'i	Lumaha'i	21015	2.11	1.82	4.28
	Kaua'i	Hanamā'ulu	22012	120.74	–1.95	1.06		Kaua'i	Kalihiwai River	21025	10.66	1.00	2.89
	Kaua'i	Hulē'ia	22015	6.00	0.05	1.32		Kaua'i	Kulihaili	21029	73.50	–2.10	1.00
	Kaua'i	Waikomo	23002	145.43	–0.77	0.07		Kaua'i	Pīla'a	21031	20.94	–0.72	1.51
	Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84		Kaua'i	Anahola	22001	50.01	1.11	4.28
	Kaua'i	Waimea River	24004	5.46	2.52	7.39		Kaua'i	Kapa'a	22004	82.97	0.18	1.24
	O'ahu	Kaluanui	31013	32.40	0.66	0.78		Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84
	O'ahu	Punalu'u	31016	36.35	1.10	1.28		Kaua'i	Hanapēpē River	23007	70.07	0.20	0.62
	O'ahu	Kahana	31018	19.21	1.62	2.08		Kaua'i	Nu'alolo	25016	0.15	1.74	0.48
	O'ahu	Hakipu'u	32001	52.14	0.55	1.58		O'ahu	Kahawainui	31007	94.14	0.55	0.35
	O'ahu	Waikāne	32002	35.06	1.06	2.40		O'ahu	Wailele	31008	482.91	–0.62	0.37
	O'ahu	Kahalu'u	32007	620.50	–0.85	0.76		O'ahu	Kaluanui	31013	32.40	0.66	0.78
	O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19		O'ahu	Hakipu'u	32001	52.14	0.55	1.58
	O'ahu	Kawainui	32013	290.27	–0.48	6.46		O'ahu	Kahalu'u	32007	620.50	–0.85	0.76
	O'ahu	Ala Wai	33007	3336.64	–2.74	0.15		O'ahu	Kāwā	32011	1157.72	–2.98	1.01
	O'ahu	Moanalua	33012	440.75	–1.46	0.47		O'ahu	Waimānalo	32015	234.00	–1.48	0.19
	O'ahu	Waikele	34010	736.01	–2.16	0.06		O'ahu	Nu'uanu	33009	2015.31	–1.87	0.46
	O'ahu	Ki'iki'i	36006	268.64	–0.73	0.18		O'ahu	Moanalua	33012	440.75	–1.46	0.47
	O'ahu	Paukauila	36007	37.88	0.04	–0.09		O'ahu	Waikele	34010	736.01	–2.16	0.06
	O'ahu	Anahulu	36008	30.79	0.27	0.16		O'ahu	Waimea River	36010	12.46	1.49	0.15
	O'ahu	Waimea River	36010	12.46	1.49	0.15		Moloka'i	Wailau	41015	0.10	2.20	0.48
	Hawai'i	Hualua	81001	49.09	–0.87	–1.55		Moloka'i	Hālawa	41021	1.12	1.85	0.37
	Hawai'i	Kumakua Gulch	81003	88.62	–0.53	–1.37		Moloka'i	Honouli Wai	42003	3.26	1.09	0.48
	Hawai'i	Waiania Gulch	81009	34.83	–0.72	–1.72		Moloka'i	Waialua	42004	5.02	1.25	0.44
	Hawai'i	'A'amakāō Gulch	81012	2.05	1.01	–1.29		Moloka'i	Kainalu Gulch	42005	10.09	0.99	0.17
								Moloka'i	Kamalō Gulch	42014	5.08	0.60	–0.15
								Moloka'i	Kawela Gulch	42015	6.17	0.42	–0.15
								Moloka'i	Pāpio Gulch	42016	3.90	0.90	0.36
								Maui	Ukumehame	61001	0.18	0.94	–0.68
								Maui	Honokōhau	61011	3.68	2.18	0.35
								Maui	Kahakuloa	62003	5.73	1.98	0.96
								Maui	Makamaka'ole	62006	7.96	0.55	0.05
								Maui	Kalae'ili'ili	62022	177.07	–0.22	–0.40
								Maui	Māliko Gulch	63001	62.72	0.35	–1.59
								Maui	Honopou	63008	12.29	0.25	0.11
								Maui	Pi'ina'au	64011	0.86	1.81	–1.57
								Maui	Wailua Nui	64014	3.64	1.59	–1.72
								Maui	Kopili'ula	64017	0.64	2.07	–1.07

Annexe 3. – Continued.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
								Maui	Waiohue	64018	0.57	1.79	–0.40
								Maui	Hanawī	64022	0.75	1.96	–1.60
								Maui	Makapipi	64023	4.64	2.15	–0.86
								Maui	Kapia	65003	4.51	1.16	–0.08
								Maui	Wailua	65007	4.74	1.20	–0.01
								Maui	Pua’alu’u Gulch	65012	1.23	–0.23	–0.47
								Maui	‘Ālelele	65020	2.03	1.94	–0.33
								Maui	Manawainui	65024	1.94	1.18	–1.73
								Hawai’i	‘A’amakāō Gulch	81012	2.05	1.01	–1.29
								Hawai’i	Waikama Gulch	81014	8.42	0.86	–0.93
								Hawai’i	Honokāne Ike	81017	0.00	1.85	–0.20
								Hawai’i	Honopue	81022	0.15	1.81	–0.17
								Hawai’i	Waimanu	81035	0.22	1.99	2.21
								Hawai’i	Ka’awali’i Gulch	82002	0.95	1.81	–1.94
								Hawai’i	Waikaumalo	82024	1.57	1.91	–1.17
								Hawai’i	Nānue	82027	0.42	1.62	–2.18
								Hawai’i	Kolekole	82033	2.64	1.75	–1.81
								Hawai’i	Pahe’ehe’e	82034	46.49	0.37	–0.59
								Hawai’i	Honomū	82035	25.86	0.04	–0.61
								Hawai’i	Mākea	82038	14.13	–2.18	–0.46
								Hawai’i	Ālia	82039	24.56	–3.40	0.02
								Hawai’i	Kawainui	82043	1.87	0.74	–0.94
								Hawai’i	Onomea	82044	27.32	–2.73	–0.57
								Hawai’i	Alakahi	82045	19.59	–2.27	–0.47
								Hawai’i	Hanawī	82046	2.59	0.75	–0.71
								Hawai’i	Kalaoa	82047	31.20	–1.65	–0.23
								Hawai’i	Pu’uokālepa	82050	92.59	–1.82	–0.23
								Hawai’i	Ka’āpoko	82051	519.70	–4.73	0.03
								Hawai’i	Kapu’e	82053	13.24	1.04	–0.96
								Hawai’i	Pāhoehoe	82054	3.98	1.05	–0.72
								Hawai’i	Pauka’a	82055	101.29	–4.46	–0.26
								Hawai’i	Maili	82057	35.24	0.19	–0.71
								Hawai’i	Pūkīhae	82059	64.90	0.07	–0.74
								Hawai’i	Wailoa River	82061	96.74	0.95	–1.30
Non-native mollusks	Kaua’i	Hanalei River	21019	7.18	1.49	3.74	Native mollusks	Kaua’i	Wainiha	21014	8.23	2.58	8.62
	Kaua’i	Kīlauea,	21028	52.05	0.58	6.65		Kaua’i	Lumaha’i	21015	10.66	1.00	2.89
	Kaua’i	Kulihaili	21029	73.50	–2.10	1.00		Kaua’i	Kīlauea,	21028	52.05	0.58	6.65
	Kaua’i	Wailua River	22008	46.60	1.03	1.58		Kaua’i	Kulihaili	21029	73.50	–2.10	1.00

Annexe 3. – Continued.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
	Kaua'i	Nāwiliwili	22013	388.71	–2.92	1.25		Kaua'i	Waipaki East	21033	37.30	–0.75	1.09
	Kaua'i	Hulā'ia	22015	6.00	0.05	1.32		Kaua'i	Kapa'a	22004	82.97	0.18	1.24
	Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84		O'ahu	Kaluanui	31013	32.40	0.66	0.78
	Kaua'i	Waimea River	24004	5.46	2.52	7.39		O'ahu	He'eia	32008	462.99	–1.53	2.96
	O'ahu	Punalu'u	31016	36.35	1.10	1.28		O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19
	O'ahu	Hakipu'u	32001	52.14	0.55	1.58		O'ahu	Nu'uanu	33009	2015.31	–1.87	0.46
	O'ahu	Waikāne	32002	35.06	1.06	2.40		O'ahu	Waikele	34010	736.01	–2.16	0.06
	O'ahu	Waiāhole	32004	30.11	1.02	1.01		O'ahu	Waimea River	36010	12.46	1.49	0.15
	O'ahu	Kahalu'u	32007	620.50	–0.85	0.76		Moloka'i	Pelekunu	41009	0.10	1.74	0.30
	O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19		Maui	Makamaka'ole	62006	7.96	0.55	0.05
	O'ahu	Kawainui	32013	290.27	–0.48	6.46		Maui	Waiehu	62008	460.94	–0.81	–0.09
	O'ahu	Waimānalo	32015	234.00	–1.48	0.19		Maui	Nua'ailua	64010	4.79	1.46	–0.03
	O'ahu	Wailupe	33005	591.72	–2.18	0.54		Maui	Pi'ina'au	64011	0.86	1.81	–1.57
	O'ahu	Nu'uanu	33009	2015.31	–1.87	0.46		Maui	Wailua Nui	64014	3.64	1.59	–1.72
	O'ahu	Kalauao	34004	1197.58	–2.01	0.58		Maui	Wailua Iki West	64015	0.94	2.26	–0.72
	O'ahu	Waiawa	34006	368.89	–0.95	0.14		Maui	Waiohue	64018	0.57	1.79	–0.40
	O'ahu	Waikele	34010	736.01	–2.16	0.06		Maui	Pua'alu'u Gulch	65012	1.23	–0.23	–0.47
	O'ahu	Mākaha	35007	400.12	–0.42	0.32		Maui	'Ohe'o Gulch	65013	0.78	1.70	–0.76
	O'ahu	Ki'iki'i	36006	268.64	–0.73	0.18		Hawai'i	Waimanu	81035	0.22	1.99	2.21
	Maui	Pi'ina'au	64011	0.86	1.81	–1.57		Hawai'i	Mākea	82038	14.13	–2.18	–0.46
	Maui	Wailua Iki West	64015	0.94	2.26	–0.72		Hawai'i	Kawainui	82043	1.87	0.74	–0.94
	Maui	Hanawī	64022	0.75	1.96	–1.60		Hawai'i	Onomea	82044	27.32	–2.73	–0.57
	Maui	Wailua	65007	4.74	1.20	–0.01		Hawai'i	Hanawī	82046	2.59	0.75	–0.71
	Hawai'i	Nānue	82027	0.42	1.62	–2.18		Hawai'i	Ka'ie'ie	82049	29.54	–0.12	–0.86
	Hawai'i	'Uma'uma	82030	1.10	1.66	–1.99		Hawai'i	Wailuku	82060	7.91	1.67	–2.32
	Hawai'i	Wailuku	82060	7.91	1.67	–2.32							
Non-native crustaceans	Kaua'i	Honopū	21002	0.28	1.49	0.36	Native crustaceans	Kaua'i	Kalalau	21004	0.37	1.37	0.63
	Kaua'i	Kalalau	21004	0.37	1.37	0.63		Kaua'i	Limahuli	21012	16.11	1.11	0.81
	Kaua'i	Waiahuakua	21008	0.56	1.55	0.83		Kaua'i	Waipā	21017	1.27	1.35	3.74
	Kaua'i	Hanakāpī'ai	21010	0.41	1.68	0.58		Kaua'i	Kalihiwai River	21025	10.66	1.00	2.89
	Kaua'i	Wainiha	21014	8.23	2.58	8.62		Kaua'i	Kīlauea,	21028	52.05	0.58	6.65
	Kaua'i	Hanalei River	21019	7.18	1.49	3.74		Kaua'i	Waipaki East	21033	37.30	–0.75	1.09
	Kaua'i	Waipaki East	21033	37.30	–0.75	1.09		Kaua'i	Moloa'a	21034	16.06	0.44	2.05
	Kaua'i	Wailua River	22008	46.60	1.03	1.58		Kaua'i	Kapa'a	22004	82.97	0.18	1.24
	Kaua'i	Nāwiliwili	22013	388.71	–2.92	1.25		Kaua'i	Wailua River	22008	46.60	1.03	1.58
	Kaua'i	Pū'ali	22014	645.63	–3.40	0.80		Kaua'i	Hulē'ia	22015	6.00	0.05	1.32
	Kaua'i	Hulē'ia	22015	6.00	0.05	1.32		Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84
	Kaua'i	Lāwa'i	23004	198.22	–0.61	1.84		Kaua'i	Hanapēpē River	23007	70.07	0.20	0.62
	Kaua'i	Waimea River	24004	5.46	2.52	7.39		O'ahu	Wailele	31008	482.91	–0.62	0.37
	O'ahu	Kahana	31018	19.21	1.62	2.08		O'ahu	He'eia	32008	462.99	–1.53	2.96
	O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19		O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19

Annexe 3. – Continued.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
	O’ahu	Waimānalo	32015	234.00	–1.48	0.19		O’ahu	Kawainui	32013	290.27	–0.48	6.46
	O’ahu	Ala Wai	33007	3336.64	–2.74	0.15		O’ahu	Ala Wai	33007	3336.64	–2.74	0.15
	O’ahu	Nu’uanu	33009	2015.31	–1.87	0.46		O’ahu	Nu’uanu	33009	2015.31	–1.87	0.46
	O’ahu	Kalihi	33011	1891.55	–1.67	0.66		O’ahu	Kalauao	34004	1197.58	–2.01	0.58
	O’ahu	Waiawa	34006	368.89	–0.95	0.14		O’ahu	Waikele	34010	736.01	–2.16	0.06
	O’ahu	Waikele	34010	736.01	–2.16	0.06		O’ahu	Waimea River	36010	12.46	1.49	0.15
	O’ahu	Waipio Naval Reservoir	34018	3604.63	–6.10	0.12		Moloka’i	Hālawa	41021	1.12	1.85	0.37
	O’ahu	Ki’iki’i	36006	268.64	–0.73	0.18		Moloka’i	Honouli Wai	42003	3.26	1.09	0.48
	O’ahu	Paukauila	36007	37.88	0.04	–0.09		Maui	Makamaka’ole	62006	7.96	0.55	0.05
	Moloka’i	Pāpio Gulch	42016	3.90	0.90	0.36		Maui	Honopou	63008	12.29	0.25	0.11
	Maui	Honokōhau	61011	3.68	2.18	0.35		Maui	Pi’ina’au	64011	0.86	1.81	–1.57
	Maui	Makamakaole	62006	7.96	0.55	0.05		Maui	Wailua Nui	64014	3.64	1.59	–1.72
	Maui	Waiehu	62008	460.94	–0.81	–0.09		Maui	Waiohue	64018	0.57	1.79	–0.40
	Maui	‘Īao	62009	402.51	–0.75	–0.13		Maui	Pua’alu’u Gulch	65012	1.23	–0.23	–0.47
	Maui	Hanehoi	63011	18.25	0.71	–0.60		Maui	‘Ohe’o Gulch	65013	0.78	1.70	–0.76
	Maui	Waikamoi	64004	0.33	2.15	–0.67		Maui	Waikapū	66010	30.78	–0.74	–0.60
	Maui	Wailua Nui	64014	3.64	1.59	–1.72		Hawai’i	Waikama Gulch	81014	8.42	0.86	–0.93
	Maui	Waiohue	64018	0.57	1.79	–0.40		Hawai’i	Honokāne Nui	81016	0.04	2.38	0.13
	Maui	Makapipi	64023	4.64	2.15	–0.86		Hawai’i	Honokāne Ike	81017	0.00	1.85	–0.20
	Hawai’i	Kūwaikahi	82007	52.41	–0.87	–0.66		Hawai’i	Waimanu	81035	0.22	1.99	2.21
	Hawai’i	Kapehu	82012	29.59	–0.82	–0.42		Hawai’i	Kapehu	82012	29.59	–0.82	–0.42
	Hawai’i	Waikaumalo	82024	1.57	1.91	–1.17		Hawai’i	Pōhakupuka	82016	6.46	1.41	–0.14
	Hawai’i	‘Opea	82028	2.52	0.11	–0.94		Hawai’i	Nānue	82027	0.42	1.62	–2.18
	Hawai’i	Hakalau	82032	4.11	1.19	–0.88		Hawai’i	‘Opea	82028	2.52	0.11	–0.94
	Hawai’i	Honomū	82035	25.86	0.04	–0.61		Hawai’i	Kolekole	82033	2.64	1.75	–1.81
	Hawai’i	Onomea	82044	27.32	–2.73	–0.57		Hawai’i	Pahe’ehe’e	82034	46.49	0.37	–0.59
	Hawai’i	Kapue	82053	13.24	1.04	–0.96		Hawai’i	Wai’a’ama	82042	37.10	–0.11	–0.47
	Hawai’i	Honoli’i	82056	7.79	1.27	–0.90		Hawai’i	Onomea	82044	27.32	–2.73	–0.57
	Hawai’i	Maili	82057	35.24	0.19	–0.71		Hawai’i	Alakahi	82045	19.59	–2.27	–0.47
	Hawai’i	Pūkīhae	82059	64.90	0.07	–0.74		Hawai’i	Hanawī	82046	2.59	0.75	–0.71
	Hawai’i	Wailuku	82060	7.91	1.67	–2.32		Hawai’i	Ka’ie’ie	82049	29.54	–0.12	–0.86
								Hawai’i	Pāhoehoe	82054	3.98	1.05	–0.72
								Hawai’i	Maili	82057	35.24	0.19	–0.71
								Hawai’i	Pūkīhae	82059	64.9	0.07	–0.74
								Hawai’i	Wailuku	82060	7.91	1.67	–2.32
Non-native insects	Kaua’i	Kīlauea	21028	52.05	0.58	6.65	Native insects	Kaua’i	Waimea River	24004	5.46	2.52	7.39
	Kaua’i	Pīla’a	21031	20.94	–0.72	1.51		O’ahu	Kaipapa’u	31010	178.91	0.43	0.82
	Kaua’i	Kapa’a	22004	82.97	0.18	1.24		O’ahu	Punalu’u	31016	36.35	1.10	1.28
	Kaua’i	Hulē’ia	22015	6.00	0.05	1.32		O’ahu	Waiāhole	32004	30.11	1.02	1.01
	O’ahu	Kaipapa’u	31010	178.91	0.43	0.82		O’ahu	Waikele	34010	736.01	–2.16	0.06

Annexe 3. – Continued.

Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2	Taxonomic group	Island	Watershed	DAR code	Human population density (persons/km^2)	Land-use PC1	Land-use PC2
	O'ahu	Punalu'u	31016	36.35	1.10	1.28		O'ahu	Anahulu	36008	30.79	0.27	0.16
	O'ahu	Kahana	31018	19.21	1.62	2.08		Moloka'i	Pelekunu	41009	0.10	1.74	0.30
	O'ahu	Hakipu'u	32001	52.14	0.55	1.58		Maui	Honokōhau	61011	3.68	2.18	0.35
	O'ahu	Waiāhole	32004	30.11	1.02	1.01		Maui	Wailua Iki West	64015	0.94	2.26	–0.72
	O'ahu	Kāne'ohe	32010	1027.14	–2.14	0.19		Maui	Pua'alu'u Gulch	65012	1.23	–0.23	–0.47
	O'ahu	Moanalua	33012	440.75	–1.46	0.47		Hawai'i	Waimanu	81035	0.22	1.99	2.21
	O'ahu	Waiawa	34006	368.89	–0.95	0.14		Hawai'i	Wailoa	81044	6.83	1.36	–0.41
	O'ahu	Waikele	34010	736.01	–2.16	0.06		Hawai'i	'Uma'uma	82030	1.10	1.66	–1.99
	O'ahu	Mākaha	35007	400.12	–0.42	0.32		Hawai'i	Hakalau	82032	4.11	1.19	–0.88
	O'ahu	Anahulu	36008	30.79	0.27	0.16		Hawai'i	Wai'a'ama	82042	37.10	–0.11	–0.47
	Moloka'i	Pelekunu	41009	0.10	1.74	0.30		Hawai'i	Kawainui	82043	1.87	0.74	–0.94
	Maui	Makamaka'ole	62006	7.96	0.55	0.05		Hawai'i	Hanawī	82046	2.59	0.75	–0.71
	Maui	Wailua Iki West	64015	0.94	2.26	–0.72		Hawai'i	Ka'ie'ie	82049	29.54	–0.12	–0.86
	Hawai'i	Wailoa	81044	6.83	1.36	–0.41		Hawai'i	Kapu'e	82053	13.24	1.04	–0.96
	Hawai'i	Waikōloa	81051	1.86	–0.33	–0.86		Hawai'i	Pāhoehoe	82054	3.98	1.05	–0.72
	Hawai'i	'Uma'uma	82030	1.01	1.66	–1.99		Hawai'i	Honoli'i	82056	7.79	1.27	–0.90
	Hawai'i	Kawainui	82043	1.87	0.74	–0.94		Hawai'i	Wailuku	82060	7.91	1.67	–2.32
	Hawai'i	Ka'ie'ie	82049	29.54	–0.12	–0.86							
	Hawai'i	Honoli'i	82056	7.79	1.27	–0.90							
	Hawai'i	Wailuku	82060	7.91	1.67	–2.32							
	Hawai'i	Hīlea Gulch	83015	0.33	1.85	–1.95							
	Hawai'i	Wai'ula'ula	85003	35.49	–0.02	–2.44							